THE OPTOKINETIC RESPONSES OF THE CRAB, CARCINUS MAENAS

W. J. P. Barnes

A Thesis Submitted for the Degree of PhD
at the
University of St Andrews

1967

Please use this identifier to cite or link to this item:
http://hdl.handle.net/10023/14855

The Optokinetic Responses of the Crab, *Carcinus maenas*

by

W.J.P. Barnes, B.Sc. (St Andrews).

Gatty Marine Laboratory and Department of Natural History,

University of St Andrews.

1967

Thesis submitted for the Degree of Doctor of Philosophy.

CONTENTS

DECLARATION

I declare that the work reported in this thesis is my own and has not been previously submitted for any other degree.

[redacted]

SUPERVISOR'S CERTIFICATE

I certify that Jonathan Barnes has fulfilled the conditions laid down under Ordinance No. 16 of the University Court, St Andrews, and is accordingly qualified to submit this thesis for the degree of Doctor of Philosophy.

[redacted]

ACKNOWLEDGEMENTS

It is a pleasure to record my thanks to Dr. G.A. Horridge, my Supervisor, for his help and encouragement throughout the last four years, to Mr. P.R.B. Shepheard for his collaboration in the experiments on the build-up of optokinetic memory, and to Dr. M. Burrows for his useful criticisms of the draft of this thesis.

ABSTRACT

The movements of the eyecups of the common shore crab, Carcinus maenas L., that occur in response to a variety of different visual stimuli, have been studied with a view to analysing the mechanisms of eye movement control in the Crustacea.

In most experiments, a light flag was glued to one of the crab's eyecups. The flag was orientated so that it partially occluded a beam of light that was focussed on a pair of photocells, mounted in opposition to one another. Flag movements thus caused changes in the amount of light reaching the photocells, whose outputs were amplified and displayed on a pen recorder.

That small eyecup movements occur in the absence of moving stimuli has been confirmed. These movements have been classified into four categories; tremor - oscillations of peak to peak amplitude 0.01°-0.2° and predominant frequency 1-3 c.p.s., which could be modified to a small extent by external stimuli; drift - slow wandering movements that mainly occurred when there were no contrasts in the visual field; saccades - spontaneous jumps whose frequency and amplitude were extremely variable; and scanning movements of amplitude 0.1°-2.0° peak to peak, and frequency 2-3 c.p.s., which were always associated with periods of leg waving.

All other experiments were directly concerned with the optokinetic responses of Carcinus, which were usually elicited by rotating a black and white striped drum around the crab. Optokinetic nystagmus consists of two phases, a slow forward phase during which the eyes move in the direction of rotation of the stripes, and a fast return phase in which the eyes are flicked back in the opposite direction. Although the evidence is by no means conclusive, it appeared that Carcinus has neither a proprioceptive nor an oculomotor feedback loop in its eye movement control system. It may thus be unable to distinguish apparent motion, induced by its own eye movement, from world motion.

Optokinetic responses also occurred to the movements of a pinlight in an otherwise dark visual field. When recorded in two dimensions on an X-Y plotter, the responses to the movement of a pinlight in a circle were seen to be approximate ellipses, though stepwise movements frequently occurred instead of diagonal movements. The possibility, suggested by this observation, that Carcinus resolved diagonal movements into their horizontal and vertical components was confirmed by the finding that the angles of the responses to diagonal movements of the pinlight depended upon the ratio of the gains (gain equals response divided by stimulus) to horizontal and vertical pinlight movements. The possibility that Carcinus uses this ability to resolve the sun or moon's motion cannot be excluded.

When one pinlight was switched off and a similar one was switched on nearby, the crab responded optokinetically, the amplitude of this response being proportional to the stimulus amplitude for apparent movements of up to 3°-4°. This suggests that movement correlation takes place primarily between closely spaced ommatidia. The responses to the movement or apparent movement of two or more lights were proportional to the shift in the centre of light intensity, an indication that the spatial resolution of the eyes is poor.

Optokinetic memory responses, which occur following shifts in the drum position that are not seen by the crab, were also studied. By varying the length of time that the crab viewed the stripes before they were moved, memory was shown to build-up approximately linearly, reaching a plateau representing a gain of between 6 and 30 after 40-100 seconds. The retention of memories allowed to build-up for different periods of time was also examined. There was no evidence for the existence of more than one memory store. A model of the control system for memory responses is proposed and tested in which the stimulus in the memory situation, the mismatch between the present and a spatially remembered version of the previous position of the stripes, is differentiated and fed into the control system for normal optokinetic responses.

Responses to step movements of the striped drum have both fast and slow components which have been identified as velocity and memory responses respectively. The responses that occurred to ramp stimuli moving at velocities below 0.005°/sec have also been shown to be memory responses. Thus memory plays an integral part in many of the optokinetic responses of *Carcinus*.

Experiments in which the eyes viewed different sets of stripes, which could be moved independently of each other, demonstrated that each eye has its own system for converting perceived motion into eye movement. Although these two systems are linked, the eyes had a considerable degree of independence during the initial part of an optokinetic response, and frequently moved in opposite directions. After a few degrees of movement, however, the eyes either came to a standstill, or moved in the direction of the slower moving of the two visual inputs, often at similar velocities. Other experiments have shown that the control systems of the two eyes are linked on the sensory side of the brain.

That the onset of the fast phase of nystagmus does not depend upon proprioceptive information from the eyes, but is centrally initiated, has been confirmed. A model is proposed in which fast phases to the left are initiated by the left eye control system, those to the right by the eye control system.

INTRODUCTION

The compound eyes of decapod crustaceans are raised on stalks, the eyecups, which are free to move in all directions relative to the carapace. Like the eyes of mammals, the eyecups of decapods exhibit a variety of oscillations over a wide frequency spectrum. These movements occur even in the absence of moving stimuli and may be conveniently classified into tremor, drift, saccades and scanning. Several different types of eyecup response can also be recognised, including the optokinetic responses, that occur following the movement of contrasting objects in the visual field.

This thesis is primarily concerned with different aspects of these optokinetic responses, though the normal movements of the eyes are also briefly considered. The approach throughout is that of control systems analysis, the formulation of a model of the reflex from exact measurements of the output (eye movement) in response to different controlled inputs (visual stimuli). No attempt has been made to describe the reflex by means of a series of equations. Rather a wide variety of different stimulus situations have been exploited in order to reveal various aspects of the nervous and muscular mechanisms involved in the optokinetic reflex.

There are several reasons why <u>Carcinus</u> was chosen for these experiments. Firstly, since the crab in its natural habitat spends long periods out of water in the intertidal zone, experiments could be performed in air without subjecting the crab to abnormal conditions. Secondly, the eyecups, unlike those of many decapods, could bear the small weight of the flag, by means of which the eye movements were recorded, without apparent inconvenience. Thirdly, the shape of the carapace and the wide separation of the eyes enabled easy clamping of the crab within the apparatus, and made possible simultaneous recording of the movements of both eyes. Finally, Carcinus is a common species and large numbers were available in the laboratory throughout the year.

Experiments on different aspects of the eye movements of Carcinus were carried out by Dr. G.A. Horridge at the same time as, but independently of, the work of this thesis, and have since appeared in print (Horridge, 1965, 1966a,b,d,e,f,g, 1967a,b, Horridge and Shepheard, 1966).

CRUSTACEAN EYE MOVEMENTS

Several distinct classes of eye movements have been described in stalk-eyed crustaceans. There are compensatory responses to tilt or rotation of the animal; eye movements of central origin that occur during walking; reflex retraction in response to touch in the region of the eyecup; maintained eye movements that occur under the influence of asymmetrical illumination; fixation movements in Squilla, and following eye movements (optokinetic responses) in response to movement or apparent movement of contrasting objects within the visual field. There are also the normal movements of the eyes, tremor, drift, saccades and scanning, which will be further described in the "Results" section of this thesis.

Compensatory responses

That decapods show compensatory eye movements in response to tilt about the pitch (transverse) axis, and roll (longitudinal) axis was first noted by Kreidl (1893) in the prawn, Palaemon, during the course of his experiments on the function of crustacean statocysts. These reflexes were further studied by Clark (1896) in the crabs Gelasimus and Platyonichus. Clark showed that the crabs compensated to tilt by moving their eyes in the opposite direction to the imposed movement, so tending to keep them in a constant position relative to the environment.

Although estimates of the extent of the eye compensation were made by Clark, and also by Schöne (1954) in Palaemonetes and Milne & Milne (1965) in a variety of decapods, only Horridge (1966e), working on Carcinus, has accurately measured the change in eye angle relative to the horizontal, for different amounts of tilt about both the pitch and roll axes. Horridge showed that Carcinus never compensates entirely for the imposed tilt but that some compensation occurs for angles of tilt of up to 70° from the crab's normal position. When

Carcinus is tilted about the pitch axis, the change in eye angle relative to the horizontal is less than 10% of the change in carapace angle for tilts of up to 20°. As the degree of tilt is increased above this angle, the degree of compensation progressively decreases. Compensation for tilt about the roll axis is not so complete and the change in eye angle relative to the horizontal is only as low as 40% of the change in carapace angle for carapace deviations of less than 10° from the horizontal.

Compensatory eye movements have also been observed in response to rotation of decapods about their vertical axes. Bethe (1897a), working on *Carcinus*, showed that the eyes move slowly in the opposite direction to the imposed rotation (the slow phase of the response), tending to remain stationary with respect to the environment. Continued rotation causes the eyes to flick quickly in the direction of the imposed rotation (the fast phase), before beginning another slow phase. In blinded animals, the response is evoked only by angular acceleration or deceleration, though responses may persist for several seconds after the cessation of rotation (Dijkgraaf, 1955). The response is thus similar to mammalian vestibular nystagmus.

The sense organs primarily involved in these compensatory eye responses are the statocysts located in the basal segments of the antennules, for reflex eye movements can be induced by direct stimulation of the statolith hairs (Schöne, 1959). Schöne showed that lateral bending of the statolith hairs of the crayfish Astacus evoked the same reflex eye movements as tilting the animal about its roll axis towards the side of the statocyst involved. Vision plays no part in these reflexes in the absence of contrasting objects in the visual field. However, all compensatory eye responses are not abolished by removing the statocysts of blinded animals, for even under these conditions some reflex eye movements occur in Carcinus when it is passively rotated upon its leg joints (Dijkgraaf, 1956a). Under these conditions the reflexes are presumed to be initiated by leg proprioceptors.

Eye movements during walking

Bethe (1897a) observed that, before moving in a particular direction, Carcinus flicks its eyes in that direction. Then, during movement, the eyes swing back and forth. Removal of the statocysts and blinding the crab failed to abolish these movements, which are thus presumed to be of central origin. Dijkgraaf, who has observed these movements in a variety of decapods, (Dijkgraaf, 1956a,b), suggests that they are initiated in close co-ordination with the turning movements of the legs, but in the absence of exact measurements of these eye movements with respect to both the crab's carapace and to the environment, it is difficult to assess their function. It seems probable that they partially compensate for body movements during walking and are thus analagous to the eye movements observed in dogfish while swimming (Harris, 1965a,b).

Reflex eye retraction

In crabs, the eyecup is generally withdrawn when it, or the surrounding carapace is roughly touched. In this reflex, first noted by MacIntosh (1860) in *Carcinus*. the eyecup flicks back into its socket by a movement away from the midline. Bethe (1897a) demonstrated that the reflex was most easily elicited by mechanical stimulation of the regions of the carapace supplied by the tegumentary nerves. These regions extend back as far as the cervical groove and overlap in the midline. Stimulation of this midline region evoked reflex retraction of both eyes, while touching, say, the left side of the carapace, caused the withdrawal of only the left eye. Following gentle stimulation, the eye was withdrawn for only a few seconds and then extended again, but stronger stimulation caused eyecup retraction to be maintained, as well as eliciting withdrawal of the ipsilateral antennule and antenna.

Burrows and Horridge (1967) have shown that the extension of the eyecup of *Carcinus* after retraction returns it to the position it occupied before withdrawal. The return is remarkably precise and thus probably involves memory of the previous impulse frequencies in the efferent neurones to the eye muscles.

When one of the statocysts of *Carcinus* is removed, the retraction reflex occurs spontaneously in the ipsilateral eye, approximately once every 13 secs. (Sandeman, 1967). This spontaneity indicates the presence of a pacemaker in the brain usually counteracted by normal sensory input.

Maintained eye movements

Many aquatic animals, including decapods which have no statocysts, orientate themselves while swimming by means of an optical mechanism called a dorsal light reaction by Fraenkel and Gunn (1940). When held at different angles to incident light, this response takes the form of a maintained movement of the eyecups, which are deflected so that the dorsal ommatidia receive equal and maximal amounts of light (Alverdes, 1926).

As well as occurring in statocystless species such as *Processa canaliculata*, maintained eye movements also occur in shrimps and prawns that possess statocysts, where they interact with the compensatory eyecup responses described in an earlier section of the "Introduction". In one such species, the prawn *Palaemonetes varians* studied by Schöne (1952, 1961), the degree of eyecup deflection depended upon the orientation of the animal with respect to gravity, being greatest when the statocysts were horizontal and therefore not affected by any shearing force, and weakest when the sensory hairs on the statocyst wall underwent maximum shearing by the statoliths.

The eyes are not completely independent of each other during this response, for a blinded eye is deflected along with the other eye in response to a laterally placed light (Schöne, 1961). Indeed, the stability of free-swimming, statocystless, shrimps and prawns depends upon the two eyes receiving equal amounts of light, for unilaterally blinded *Palaemonetes* rotate continuously about their roll axes when their statocysts have been removed (Schöne, 1952). These eye responses have not been observed in crabs.

Fixation movements

The only crustacean in which fixation movements of the eyes have been described is the mantis shrimp, *Squilla*. Demoll (1909) observed that, when a ball of black paper held on a glass rod was moved towards the animal, the eyes converged; when the object was withdrawn, the eyes diverged. In all situations, the eyes were orientated so that the anteriorly facing ommatidia were pointed at the object. Binocular depth perception of vertical objects should thus be possible. However, since *Squilla* always touches its prey with its antennules before striking (Schaller 1953), there is no behavioural evidence for such depth perception, at least in prey capture.

Optokinetic responses

The following movements of the eyecups of decapod crustaceans that occur in response to movement of contrasting objects in the visual field have been more extensively studied than any of their other eye movements. In almost all of these experiments, the stimulus of preference has been a vertically striped drum which is rotated around the vertical axis of the animal. The eyecups follow the movement of the stripes, flicking back at intervals to their starting position. This response is termed optokinetic nystagmus and consists of two phases; a slow phase during which the eyes move in the same direction as the drum, though at a lower velocity, and a fast phase, where the eyes are returned quickly to approximately their initial position by a movement in the opposite direction to that of the drum.

The complete optokinetic response with both slow and fast phases probably never occurs during normal life. However, the optokinetic response of decapods and the equivalent optomotor response of insects, where the whole animal follows the stimulus rather than just the eyecups, are so consistent and so easily elicited that they have been utilized in experiments on many aspects of compound eye physiology, including spectral sensitivity, intensity discrimination, acuity and the mechanism of movement perception. Experiments such as these, in which the optokinetic response is used as a tool rather than studied as such as in this thesis, will be described in a subsequent section of the "Introduction".

The size of the moving field seems to play an important role in the optokinetic response. Von Buddenbrock and Friedrich (1933), working with Carcinus, and Kunze (1963, 1964), working with Uca and Ocypode, have measured the minimum extent of a moving field of stripes necessary to induce optokinetic nystagmus. Using the occurrence of fast phases as a measure of the response, they showed that reduction of the horizontal extent of the moving field to 100° abolished the response in all three species. In Uca and Ocypode at least, reduction of the vertical extent of the moving field had less effect for, unless the area between 5° below and 20° above eye level was covered, the response was unchanged.

Covering all of the area within these limits completely abolished the response.

When, however, the movements of an unrestrained eye are monitored accurately as in the work of Horridge, following movements of the eyecups, though not fast phases of nystagmus, can be recorded in response to horizontal movements of a single pinlight subtending only $\frac{1}{4}^{\circ}$ at the crab's eye (Horridge, 1966d on Carcinus). Such a stimulus excites far fewer ommatidia than does a moving field of stripes 100° in extent. Measurement of the velocity of the following movements of the eye (slow phase of nystagmus) is thus a much more sensitive measure of the response than is the occurrence of a fast phase. Although the appropriate experiments have not been carried out, there thus seems no good reason why following responses should not be obtained to movements of fields of stripes of less than 100° horizontal extent. However, stationary contrasting objects would have to be absent from the visual field, for such contrasts have been shown to inhibit the crab's response to a moving pinlight (Horridge, 1966d).

As well as this capacity to follow the movement of small lights, the eyes of Carcinus also have an extraordinary sensitivity to very slow movements, for the eyecups respond optokinetically to constant velocity movements of striped drums (Horridge and Sandeman, 1964) and pinlights oscillated sinusoidally (Horridge, 1966d) at velocities as low as 0.003°/sec. Indeed, the highest eyecup velocity: stimulus velocity ratio is obtained to stimulus velocities of about 0.01°/sec, only slightly greater than the mean speed of the sun and moon across the sky.

It is thus natural to consider whether the optokinetic response plays any part in orientation or navigation by the sun or moon. Though the littoral amphipods _Talitrus_ and _Talorchestia_ can navigate towards or away from the sea in the absence of any landmarks except the sun (Pardi and Papi, 1961), there is, to date, no evidence for such navigation by _Carcinus._ However, Horridge (1965, 1966e) has shown that, in the absence of stationary contrasts in the visual field, the eyecups of _Carcinus_ will respond optokinetically to the movement of the sun across the sky. The accuracy with which _Carcinus_ follows lights subtending small angles at its eye, and its ability to measure the angle of movement of such a light, a necessary prerequisite for navigation, are two of the topics further studied in this thesis.

Superimposed upon all these optokinetic responses are the normal movements of the eyes, including tremor of amplitude 0.05°-0.2° peak to peak and frequency 2-5 c.p.s. (Horridge and Sandeman, 1964, Horridge, 1966f). This means that low velocity stimuli must be averaged over several seconds before movement can be deduced. It is thus not surprising that _Carcinus_ has been shown to have a memory of past visual input which is revealed in "optokinetic memory" responses (Horridge and Shepheard, 1966, Horridge, 1966a,b). In order to elicit such a memory response, the crab is placed in a stationary drum, which is moved during a period of time (which may be a few seconds or even several minutes) that the drum illumination is turned out. When the light is turned on again, the eyes are found to move in the same direction as the drum was moved, but never through as great an angle. For such a response to have taken place, it is necessary for the crab to have correlated the present position of the drum with a memory of its previous position, the mismatch between the two causing the response.

For small movements of the drum during dark periods of a few seconds, the response is usually 70-80% of the stimulus. As the length of the dark period is progressively increased, the response falls off, until, with a dark period of 10 minutes, it is only 40% of the stimulus. The memory of the initial drum position thus decays gradually with time, but lasts for at least 20 minutes, since appreciable responses have been obtained after dark periods of that length. Experiments on the build-up of optokinetic memory with time, and the retention of memory built-up to different extents, which show that Carcinus, unlike mammals, does not have both a short and long term memory, are described in this thesis, and in a recent review by P.R.B. Shepheard, my collaborater in these experiments (Shepheard, 1966).

When the drum is moved in the dark through progressively larger angles, there comes a time when the crab confuses different stripes with each other, and responds in the opposite direction to that in which the drum was moved. The angle at which this reversal of the response occurs gives an indication of whether the crab perceives the edges or the areas of the striped pattern. Horridge (1966b) has shown that, in *Carcinus*, this response reversal usually occurs in an intermediate position between the theoretical reversal positions for area perception and edge perception, demonstrating that the crabs take account of both areas and edges. When, however, the eye that sees the stripes is fixed so that it cannot tremor, the other eye being blind and free to move, the response reversal occurs at the position expected if only areas were perceived. As a further control, Horridge then oscillated the drum at approximately eye tremor amplitude and frequency. The initial reversal position was restored showing that eye tremor accentuates the perception of edges, and thus plays an important role in vision.

Other aspects of the optokinetic response have received less attention. Though Horridge and Sandeman (1964) made the assumption that the eyes of *Carcinus* were absolutely linked together for all optokinetic responses, they never recorded the responses of both eyes simultaneously. All binocular effects are thus largely undescribed. Similarly, the mechanism of fast phase initiation is unknown, beyond the fact that it does not depend upon proprioceptive feedback (Horridge and Sandeman, 1964). These two topics are further considered in this thesis.

A detailed description of aspects of the optokinetic response which pertain particularly to experiments described in this thesis is given in the "Results" section.

ELECTROPHYSIOLOGICAL AND ANATOMICAL STUDIES

Although accurate observation or recording of eye movements during optical stimulation by moving contrasts has been the most widely used method of studying the optokinetic response of decapods, considerable insight into the mechanism of the response has also been gained by electrophysiological and anatomical investigations.

The complete eye assembly of decapods is complex, consisting of five skeletal elements under the control of thirteen pairs of muscles in the only two species studied in any detail, Callinectes (Cochran, 1935) and Carcinus (Horridge and Sandeman, 1964, Burrows and Horridge, 1967). Anterior to the brain is the median plate which is moved about the main body skeleton by three pairs of muscles, numbers 15, 16 and 17 (Cochran's terminology). Articulating with this plate are the elongated eyestalks which project laterally on either side. They are attached distally to the main body skeleton by a muscle (No. 18), contraction of which causes rotation of the eyestalk. The eyestalks are completely enclosed within a fold of exoskeleton and only the eyecups, which are borne on the distal ends of the eyestalks, are visible protruding from their sockets in intact crabs. Movement of the eyecup about the eyestalk is affected by nine muscles (Nos. 19a, 19b, 20a, 20b, 20c, 21, 22, 23a, and 23b). The eyestalk-eyecup joint is flexible, allowing limited movement in all planes.

The action of the eyecup muscles of Carcinus and their histology and innervation has been examined by Burrows (Burrows, 1967a, b; Burrows and Horridge, 1967). All of the muscles involved in the optokinetic response consist of fibres of two basic structural types which somewhat resemble the Felderstruktur and Fibrillenstruktur of vertebrate muscle fibres, though many intermediates are also found. Each muscle is supplied by both a slow and a fast axon, the two axons tending to innervate separate fibres, but with some overlap. There is no evidence for inhibitory innervation. Electrical activity associated with the firing of the slow and fast axons has been recorded both extracellularly and intracellularly, the responses to slow and fast axon activity being termed tonic and phasic respectively.

Recordings of the electrical activity of different muscles during movement of the eyecup have shown that slow, small movements of the eye are brought about by tonic activity, which also controls eye position in space. Large amplitude and rapid movements of the eye, on the other hand, are brought about by activity in the phasic system.

During the slow and fast phases of optokinetic nystagmus, each muscle has a characteristic pattern of activity which is different from that in most other muscles. For instance, during the optokinetic response in which the slow phase movement is away from the crab's midline, both the tonic and phasic activity of muscle 20a, the muscle primarily responsible for the slow phase movement in this direction, increase as the slow phase progresses, but are centrally inhibited just before the onset of the fast phase. In muscle 21, however, there is no activity during a slow phase of nystagmus in this direction, though a burst in both tonic and phasic fibres occurs during the subsequent fast phase. Although other muscles (Nos. 19b, 22, 23a and 23b) also fire during fast phases in this direction, phasic activity in this muscle is thought to be the prime cause of the fast phase movement towards the crab's midline. During optokinetic nystagmus in the opposite direction (slow phase towards midline), the slow horizontal movement towards the midline is correlated with increased activity in muscles 19b and 21, while the fast flick-back away from the midline is correlated with increased activity in muscles 20a and 22. Other muscles, notably 20b, 20c, 23a and 23b are active during the slow phases of nystagmus both towards and away from the crab's midline, but, since they only fire tonically, their role in this response is probably only a passive one, perhaps the maintenance of eye posture.

Lesion experiments in *Carcinus* by Bethe (1897a) and Sandeman (1964), and recordings of the electrical activity of single units in the oculomotor nerve of *Goniopsis* (Waterman and Wiersma, 1963) and *Carcinus* (Horridge and Sandeman, 1964), have shown that all the efferent nervous pathways of the optokinetic response are in the oculomotor nerve. The motor information to those eye muscles involved in the retraction reflex, on the other hand, is carried in the optic tract (Sandeman, 1964), contra Bethe (1897a). Burrows (1967b) has confirmed Sandeman's conclusions and has shown that two axons are involved in the protective retraction. The larger of these fibres innervates muscle 19a, which is inactive during all optokinetic responses, and some fibres in muscles 19b and 20a. The smaller axon innervates fibres in muscles 18, 20b, 21 and 22. The protective retraction of the eye is thus associated with activity in seven muscles.

From this description, it can be seen that muscle 21 is associated with an optokinetic movement of the eye towards the crab's midline, and also a retraction response in which the eye moves away from the midline. It is thus possible for one muscle, in conjunction with different patterns of activity in other muscles, to be involved in movements in opposite directions. Interpretation of eyecup muscle activity therefore becomes intelligible only if a group of muscles, rather than the individual muscles themselves, are regarded as functional units.

Afferent visual responses have also been studied in a number of decapods (Waterman and Wiersma, 1963), but especially in the crab, Podophthalmus (Waterman, Wiersma and Bush, 1964) and the crayfish Procambarus (Wiersma and Yamaguchi, 1966, Wiersma, 1967). These investigators used single unit recording techniques and positioned their electrodes on the longest part of the optic tract, which is commonly called the optic nerve.

Previous anatomical studies by Bethe (1895, 1897a,b) and Hanström (1924, 1926) have shown that this part of the optic tract is a very central part of the nervous system for, between it and the ommatidia, are four optic ganglia, the lamina, medulla externa, medulla interna and medulla terminalis. By the use of methylene blue (Bethe) and Golgi silver staining techniques (Hanström), the pathways of a few fibres have been worked out. Most fibres run only from one layer to the next (or the reverse), but a few were seen to bypass the more central ganglia and travel straight to the brain. A recent electron microscope study of the optic lamina of the lobster, Homarus, by Hâmori and Horridge (1966a,b,c,d) has shown, however, that no retinula cell axons penetrate beyond the lamina. Therefore all electrical recordings must be from second or higher order fibres.

Some fibres traced by Bethe crossed from one eyestalk to the other. Fibres such as these probably account for the visual activity of contralateral origin recorded in the optic nerve of Podophthalmus by Wiersma, Bush and Waterman (1964).

The units found in these investigations fall into several distinct classes. Sustaining fibres which change their firing frequency in response to changes in light intensity were found readily in all species investigated. They behave as light level recorders though show some adaptation over long periods of time. In the crayfish, fourteen distinct types have been distinguished on the basis of the size and position of their receptive fields, which usually cover a considerable proportion of the total visual field of the eye. These fibres also respond to moving shadows and sometimes show "on" and "off" effects, particularly if stimulated by two light sources, one of which is shining on the border of the fibre's receptive field.

Movement fibres were also frequently found. Though more erratic than sustaining fibres and therefore more difficult to study, three types could be distinguished in *Podophthalmus*, responding to fast, medium and slow movement respectively. Many of these fibres also gave noticeable responses when the light was turned out, and some gave both "on" and "off" responses. The commonest of these three types, the medium movement fibres, responded maximally to movement of the light at velocities between 0.2°/sec and 0.5°/sec, and showed little or no adaptation. Fibres of this type were usually directionally sensitive and had small receptive fields, 30-45° in extent. Less common were fast movement fibres, which responded maximally to stimuli moving at 7-8°/sec, and showed considerable adaptation, some even behaving as novelty units. Slow movement fibres, on the other hand, were most sensitive to velocities of 0.01-0.02°/sec, firing irregularly in response to higher velocity stimuli.

Dimming fibres were occasionally encountered in *Procambarus* and *Podophthalmus.* They responded to darkness in much the same way as the sustaining fibres did to increased illumination. A further class of units, *"space constant" fibres,* were characterised by receptive fields which changed in size with the position in space of the animal. For instance, one particular fibre of this class, found in *Panulirus,* had a receptive field which effectively rotated with any rotation of the eye about either the roll or tilt axis, so that the position in space of the receptive field remained constant. In other respects, these fibres were normal sustaining or movement units. Yet other fibres were found to be of mixed modality, having mechanoreceptive as well as visual inputs.

It has also been shown that fibres of most, if not all, of these classes provide centrifugal input for the optic ganglia of the other eye. Integration of the inputs from the two eyes thus probably occurs in the optic ganglia as well as in the brain. The relation of all these classes of units to the optokinetic response is more difficult to assess, for striped drums, which evoke the best optokinetic responses, have not been used as stimuli in these experiments. Nevertheless, apart from the absence of units which could account for the optokinetic responses to stimulus velocities of 0.001°/sec to 0.005°/sec, it seems unlikely that there are any important classes of units not yet discovered. The movement fibres described above thus probably form the afferent pathway of the optokinetic reflex, though other classes of units may also be involved to some extent.

THE OPTOKINETIC RESPONSE AS A TOOL IN INVESTIGATIONS INTO THE PHYSIOLOGY OF PHOTORECEPTORS

Since the optokinetic response of decapods and the equivalent optomotor response of insects are two of the most consistent and easily elicited reflexes involving vision by means of compound eyes, they have been used as a tool in many investigations into different aspects of compound eye physiology. The two most important of these studies concern the acuity of the compound eye and the formal structure of the mechanism for the perception of movement respectively. These two topics will be considered in most detail, though two other topics, light intensity discrimination and colour perception, which have also been studied by the use of the optokinetic response, will also be briefly discussed.

Intensity discrimination

This function has been studied in several species by decreasing the contrast between the "dark" and the "light" stripes of a vertically striped drum and measuring the least difference in intensity that induces an optomotor or optokinetic response. The result is most conveniently expressed as a Weber fraction, which is the ratio of the just noticeable difference in stimulus intensity to the prevailing intensity.

The intensity discrimination of the fly Drosophila, as measured by this method, is poor even at its best (Hecht and Wald, 1934), the Weber fraction only falling to 150% at high prevailing intensities of illumination. The minimum values for the crab, Goniopsis, measured by Barber and Waterman (Waterman, 1961), and the fly, Musca, calculated from data given by Fermi and Reichardt (1963), are much lower, being 1.2% and 1% respectively. The discrimination of Goniopsis and Musca is thus equivalent to that of man, where the minimum value obtained by psychophysical experiments is 1% (Bartley, 1951).

Measurements have also been made of the light threshold using the optomotor response as a criterion of discrimination. Fermi and Reichardt (1963) obtained an optomotor reaction in *Musca* when the mean brightness of the striped pattern was 2.2×10^{-3} lux. From calculations which take into account the aperture and effective angular acceptance of the ommatidia and the spectral distribution of pattern luminance, they estimate that, during a threshold optomotor response, an average of six 555 mu light quanta per second are available for absorbtion by the photopigment of a single rhabdomere. The threshold of the optomotor response of the locust, *Schistocerca*, on the other hand, is much higher, for no reaction was discernable when the average pattern luminance was decreased below 3×10^{-1} lux (Thorson, 1966a).

The only crustacean investigated in this way, the crab *Carcinus* by Horridge (1966d), appears to have an extremely low visual threshold, for eye responses were discernable to a pinlight oscillated sinusoidally, even when its intensity was reduced, by means of neutral density filters, to below 10^{-5} lux. This figure agrees well with the threshold value of 10^{-5} - 10^{-6} lux obtained by Waterman et al. (1939) for the vertical migrations of deep-water planktonic Crustacea.

Spectral sensitivity

Schlieper (1927) used the optokinetic response of the crab, *Carcinus*, to test its visual perception of colour, but failed to obtain any responses to a rotating field of alternating grey and coloured stripes. This work was repeated by Von Buddenbrock and Friedrich (1933), who used coloured stripes of equal relative brightness, and found that *Carcinus* could distinguish between yellow and blue. Using the same techniques, Schegtendal (1934) showed that *Crangon crangon* and *Palaemon squilla* were also specifically colour sensitive.

Recently, Horridge (1967b) has studied the spectral sensitivity of *Carcinus*, using a moving light source as a stimulus rather than a striped drum. By means of a range of interference, neutral density and polaroid filters of known absorbtion characteristics, he has plotted spectral sensitivity curves for the perception of movement of both horizontally and vertically polarised light in two directions. The peak sensitivity to movement occurred at 508mu, irrespective of the direction of movement or the plane of polarization of the light. However, the sensitivity to light at 439 mu (blue light) and at 650 mu (red light) was changed both by rotating the polaroid filter through 90° and by moving the light stimulus vertically instead of horizontally.

From this data, Horridge has built up a model of the connections between the primary receptors which allows independent discrimination of colour, plane of polarisation and direction of movement of a light source. Though the evidence for this particular set of connections is slight, particularly as it involves 8 retinula cells per ommatidium rather than 7 as are present in Carcinus, the experimental results cannot be interpreted in any way which involves the presence of less than two visual pigments, one more sensitive to blue light than red, the other more sensitive to red light than blue.

Acuity

Acuity, as usually defined, is a measure of the angle subtended at the eye by two objects which can just be distinguished from each other. When, however, it is measured by means of the optokinetic response, temporal as well as spatial parameters of the stimulus are involved, since the objects must be moving before responses are obtained. These experiments, in which the criterion of acuity used is the smallest pattern repeat distance of a moving striped pattern to which the animal responds optokinetically, are thus best considered to be measurements of motion acuity.

Hecht and Wolf (1929a,b) found that the acuity of the honey bee, as measured by this method, was strongly dependent upon pattern illumination, though a plateau of maximum acuity existed where further light intensity increases had no effect. They showed that there was a close correlation between maximum acuity and minimum ommatidial separation, areas of the eye in which the interommatidial angle was smallest having the highest acuity. In these investigations, a minimum interommatidial angle of approximately 1° was found to correspond with a minimum visible pattern repeat distance of 2°. Similar experiments on the fly, *Drosophila* (Hecht and Wald, 1934, von Gavel, 1939), and on the crab, *Uca* (Clark, 1935) led to the same overall conclusions, minimum interommatidial angles of 4.2° *(Drosophila)* and 2° *(Uca)* corresponding with minimum visible pattern repeat distances of 18.6° and 8° respectively.

Recent investigations have, however, shown that the relationship between acuity and the angular spacing of the ommatidia is more complex than this, for in both the fly, *Musca* (McCann and MacGinitie, 1965), and the locust, *Schistocerca* (Thorson, 1966a), acuity is diminished when the eyes are dark adapted. Such a change does not, of course, alter the interommatidial angle. However, both Vowles (1966) on the fly, *Musca* and Tunstall and Horridge (1967) on the locust, *Locusta*, have shown electrophysiologically that dark adapted ommatidia have a greater angle of acceptance than light adapted ones. It is thus probable, as Götz (1964, 1965) suggested, that acuity is governed by the angle of acceptance, which is a property of the optical pathway of the ommatidia, and defined as the angular width of the ommatidial directional sensitivity curve at half of its maximum height. In some species, however, the individual rhabdomeres are not fused into a central rhabdome, and those of the flies *Musca* and *Calliphora* at least are known to have different visual axes (Kuiper, 1962). In these insects, therefore, the smallest effective unit determining the resolution of the eye will be the angle of acceptance of a single retinula cell rather than the angle of acceptance of the whole ommatidium.

Visual acuities measured in this way vary over a broad range. The minimum pattern repeat distance resolved by the prawn, *Lysmata* is 26° (Hassenstein, 1954), whereas the bee, *Apis*, as described above, can resolve stripes of pattern repeat distance 2°. Though resolution of stripes with a pattern repeat distance of 0.3° has been claimed on electrophysiological evidence by Burtt and Catton (1961a,b, 1962a,b) for the locust eye, Palka (1965) has shown that these responses were due to events occurring at the edge of the window behind which the stripes were moved, and thus bear no relation to visual acuity.

Movement perception

In recent years, analysis of the optomotor response of the beetle, *Chlorophanus* has led to the formulation of a model for the perception of movement by the compound eye (Hassenstein, 1951, 1958a,b, 1959; Hassenstein and Reichardt, 1956; Reichardt, 1957, 1961, 1962; Reichardt and Varjú, 1959; Varjú, 1959).

In these investigations, the beetle was suspended by its head, thorax and abdomen and held a "Y-maze globe" between its feet. This globe was composed of six pieces of straw which met at four points forming three angles of 120° each. As the beetle crawled, the globe rotating beneath it, it arrived every few steps at a Y-shaped fork in its path. The beetle's tendency to turn left or right at these forks depends upon movement in the visual field, and was quantified as follows

$$\text{Turning tendency } (R) = \frac{W - A}{W + A}$$

- where W was the number of choices "with" and A the number of choices "against" the direction of movement of the visual field.

The artificial environment consisted of one or more drums which were rotated around the stationary animal. In the most sophisticated experiments, the innermost drum was black and had vertical slits, separated by angular distances equal to those between adjacent ommatidia. This made possible stimulation of discrete vertical columns of ommatidia, by either increases or decreases in light intensity.

From these experiments the following facts emerged:

(i) Successive stimulation, with either a light intensity increase or a light intensity decrease of two adjacent or subadjacent vertical columns of ommatidia induced a positive optomotor response.

(ii) Successive stimulation, with either a light intensity increase or a light intensity decrease of a single vertical column of ommatidia, or two vertical columns separated by two or more other columns, gave no response.

(iii) Stimulation of a vertical column of ommatidia with a light intensity increase followed by stimulation of the adjacent column with a light intensity decrease (or the reverse), induced a negative optomotor response.

(iv) Successive stimulation of several vertical columns of ommatidia induced a larger response than successive stimulation of just two columns. It became apparent that this reaction was the sum of the constituent partial reactions. Similarly, when the dorsal part of the eye saw a pattern moving in one direction, the ventral part a pattern moving in the other, there was no response, the conflicting stimuli balancing out.

(v) The strength of the turning tendency depended on the velocity of rotation of the drum, maximum responses being obtained when two discrete stimuli were separated by 0.25 secs. This is equivalent to a drum velocity of approximately 30°/sec.

(vi) At constant stimulus velocity, the strength of the turning tendency depended on the intensity of illumination of the drum, the response being proportional to the product, not the sum, of the two separate intensities with which adjacent columns of ommatidia were stimulated.

(vii) If the rotating cylinder was stopped suddenly, the reaction fell slowly to zero, dropping to one third of its original amplitude within 5-8 secs.

Hassenstein and Reichardt's model for the mechanism of movement perception, based on these results, made no attempt to represent neuron pathways. It was a mathematical description of the interaction of the signals from an adjacent or subadjacent pair of ommatidia (see results (i) and (ii) above), and was assumed to be reduplicated over the whole eye. Result (iv) indicated that the output of such an interacting pair of ommatidia had to be summed with the outputs of all the other pairs to give the turning tendency of the beetle.

The most interesting step in this model is the interaction of the after-effect of stimulation of one ommatidium (called A) with the signal from the next ommatidium (called B), and the reverse, since optomotor responses can occur in both directions. That this interaction is a multiplicative one is indicated primarily by result (vi), but also by results (i) and (iii) which show that the direction of the optomotor response is governed by the multiplication rule. For example, successive stimulation of A and B with light intensity increases (two positive stimuli), or light intensity decreases (two negative stimuli) induced a positive response, while stimulation of A with a light intensity increase, followed by stimulation of B with a light intensity decrease (one positive and one negative stimulus), induced a negative response.

This multiplication element is followed by a subtraction stage, where the products of the multiplication of the after-effect of stimulation of A with the signal from B, and the reverse, are subtracted from each other to give the output of the model. Linear and low pass filters, inserted to account for attenuation of the input, complete the model, the time constants of these filters being indicated by results such as (v) and (vii).

This model has since been successfully tested using a variety of techniques on several other insects, including the flies Drosophila (Götz, 1964, 1965) and Musca (Fermi and Reichardt, 1963; McCann and MacGinitie, 1965) and the locust Schistocerca (Thorson, 1964).

However, a recent analysis of the optomotor response of the locust Schistocerca, by Thorson (1966a,b) leads to criticism of this model on several counts. Thorson measured the isometric neck torque of the locust in response to oscillation of a striped drum, and confirmed his earlier finding (Thorson, 1964) that the Hassenstein-Reichardt model correctly predicted the gross gain and phase relations of the locust response to a sinusoidal stimulus. However, he found that this model was not an appropriate description of his data since the low frequency gain and phase measurements were due, not to the multiplicative and subtractive interaction of receptor channels, but to intensity-dependent photoreceptor adaptation. Similarly, at high frequencies the increase in phase lag and decrease in gain were better accounted for by a time and frequency dependent modulation of the response, than by any properties of the model. Further, Thorson showed that other models involving interaction of receptor channels via lateral shunting inhibition were, under certain conditions, indistinguishable from the Hassenstein-Reichardt model.

Therefore, although the Hassenstein-Reichardt model has certainly not been shown to be an inappropriate description of events occurring during motion perception, other models must also be considered. Also, great care must be taken to ensure that data from experiments involving the responses of whole animals relates to movement perception, and not, for instance, to photoreceptor or muscle dynamics.

MATERIALS AND METHODS

THE ANIMALS

The shore crab *Carcinus maenas* L. used in this study is a common intertidal and shallow water species. Stocks of crabs were kept in aerated aquaria at the Gatty Marine Laboratory and were fed occasionally with mussels. They appeared to thrive under these conditions.

Male crabs, six or more centimetres across the carapace, were used whenever possible, females or small males being used in only a few experiments. The only animals rejected were those infected by *Sacculina*, those with damaged eyes and those with small bivalve molluscs within their eye sockets, since the molluscs either inhibited or prevented eye movements.

THE PREPARATION

In all the experiments, the crabs were held firmly in a screw clamp which grips them on either side of the carapace dorsal to the legs. Their orientation with respect to gravity was normal, and all appendages were free to move, though unable to touch the ground. The clamp was probably just within the field of vision of the crab, although it did not interfere with vision or eye movements. All experiments took place with the crab in air, a perfectly natural situation for an intertidal species. The crabs were kept in a moist condition throughout the experiments and usually responded well for many hours.

Light flags (weight 5 mg) were made from a 4 mm square piece of black paper and a 25 mm length of stiff nylon fishing line. A flag was secured to the crab's eyestalk with warm insect wax (beeswax, lanolin and resin mixture) which had to be as cool as possible when applied. The flag lay behind the eye above the crab's carapace. It did not interfere with eye movements in any way and was invisible to the crab.

In some experiments one of the eyes was reversibly blinded by painting it over with two coats of quick drying matt black enamel paint. The success of this procedure was checked by covering the other eye with a segment of a ping pong ball and slowly rotating a striped drum about the crab; if the eye was blind no eye movement resulted.

In other experiments, a seeing eye was fixed relative to the carapace with plaster of Paris. Care was taken to ensure that the eye was fixed in its normal position and that the plaster did not cover any of the ommatidia.

THE APPARATUS

Recording of eye movements

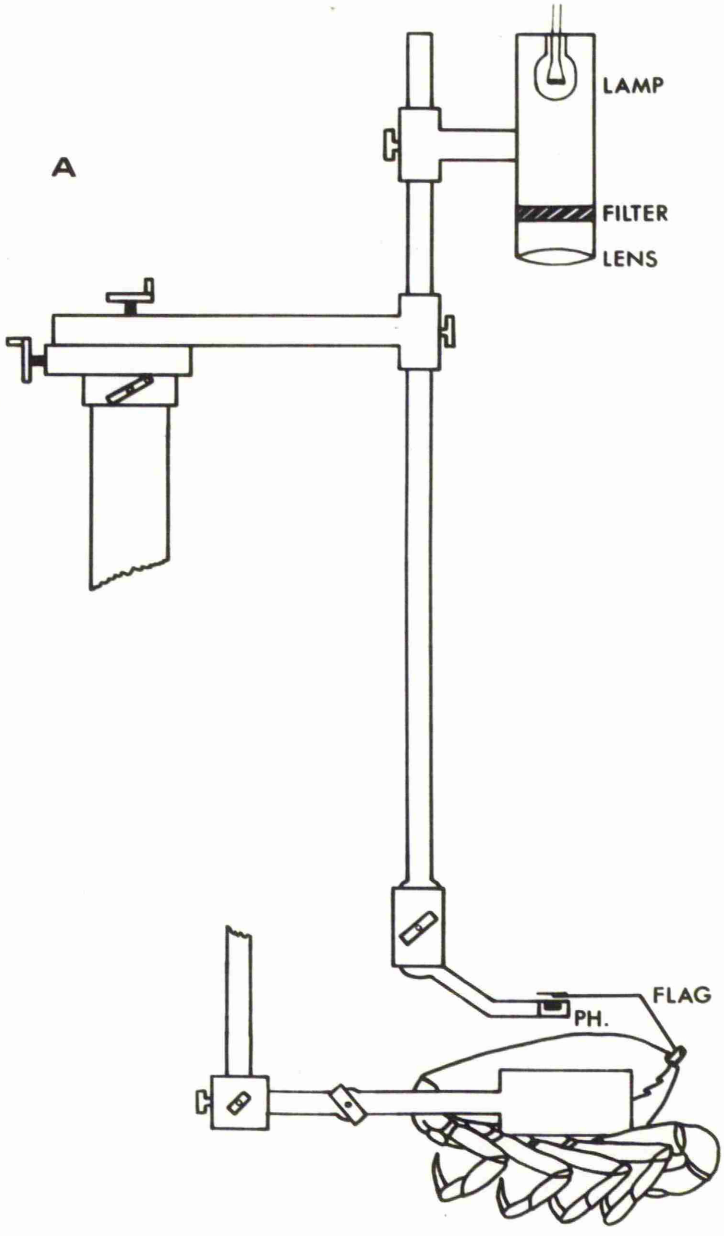
A considerable amount of time was spent in search for an accurate and convenient method of recording the eye movements of Carcinus. After many comparatively unsuccessful methods had been tried, a photocell and lamp unit was devised which enabled accurate measurement of eye movement down to 0.01°. Infra-red light from a projector lamp was focussed by a lens onto a pair of photocells mounted in opposition to one another. The whole unit was mounted above the crab so that the flag on the crab's eye partially occluded the photocells. Flag movements thus caused changes in the photocells' output which were amplified and displayed on a D.C. pen recorder (Fig. 1).

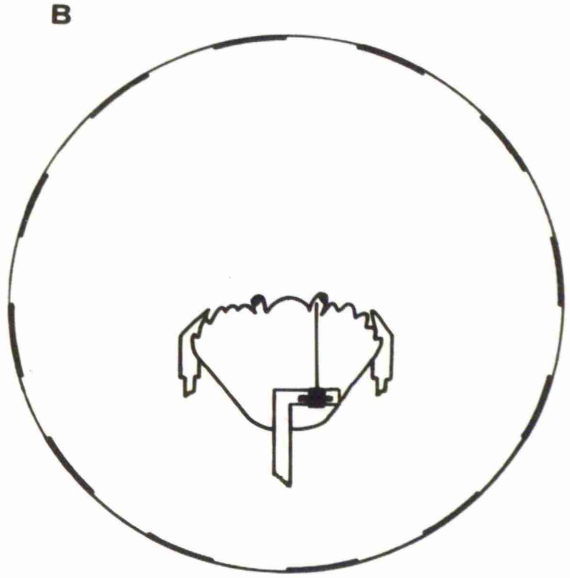
The pair of photocells used was a composite miniature unit (Texas type LS 221) 10 mm long and 2½ mm wide. It was excited by light from a 15 watt, solid filament Tungsten projector lamp, passed through an infra-red filter and focussed by a lens onto the photocells. The lamp filter and lens were mounted together in a light-proof lamp-house. The lamp-house and the probe holding the photocells were firmly mounted together on the same support, which was attached to a calibrated lathe traverse bed on a Palmer screw stand. The photocell and lamp unit could thus be moved together in three directions, enabling easy centring of the photocell under the flag on the crab's eye. This arrangement ensured that, after initial adjustment, the light beam was always focussed evenly on the photocells, and the crab was not moved during an experiment.

The output from the photocells was fed into a Devices type R2 DC pen recorder, which is characterized by a frequency response of up to 60 c.p.s. and by negligible drift when used in conjunction with a constant

FIGURE 1.

Arrangement for recording eye movements. The crab was held in a clamp so that its eyes were in the centre of the drum. A flag on the crab's eye partially occluded a pair of miniature photocells (PH) on which a beam of infra-red light was focussed by a lens. The photocells and the lamp were attached to the same support which could be adjusted in three dimensions. The photocell outputs were fed into a D.C. pen recorder, omitted from the figure for simplicity. A. side view, drum omitted from figure. B. top view.


A
LAMP
FILTER
LENS
FLAG
PH.


B

voltage transformer. This enables eye movement to be recorded with considerable accuracy, as eye tremor is only 1-3 c.p.s. The sensitivity of this device may be changed within the limits of 0.2° and 10.0° of eye movement per cm by changing the amplification of the recorder and the flag length. The photocells were calibrated directly before and after each experiment by moving the photocell unit under a stationary flag by equal steps, as measured by the calibrated lathe transverse bed. This method of recording eye movements was developed in association with my supervisor Dr. Horridge, who used it in his optokinetic experiments (Horridge 1966a,b,c,d,e,f.).

When the movement of both eyes was recorded simultaneously, a pair of photocell-lamp units of similar sensitivity were used side by side in the usual way, their outputs being recorded on a Devices type M4 four channel pen recorder.

For recording of eye movements in two dimensions, a vertical as well as a horizontal flag was attached to the crab's eye, the horizontal eye movements being recorded as usual, while vertical ones were recorded by a horizontally mounted photocell-lamp unit. The outputs of the photocells were fed into the X and Y axes of a Bryans model 22021 X-Y plotter, via Telequipment type 43B differential amplifiers backed off by HT batteries.

In a few experiments, a nylon bristle was attached to the eyestalk, and gross eye movements were measured directly with a protractor.

Optokinetic stimuli

Optokinetic responses are most easily induced in crabs by clamping the animal at the centre of a vertically black and white striped drum, and rotating the drum around the crab at a velocity between .01° and 10°/sec. The eyes follow the movement of the drum, flicking back at intervals to their starting position.

The drum used in many of these experiments was 10 ins. high and 14 ins. in diameter and was made of thick white card with painted black stripes (Fig. 1). The stripes subtended 15° at the crab's eye (i.e. stripe repeat distance = 30°), an angle shown by von Buddenbrock and Friedrich (1933) to be within the range giving maximal optokinetic responses in Carcinus.

Plain white drums and drums with periodicities of 360°, 180° and 8.5° (two, four and eighty-five black-white edges respectively) were substituted for the 30° drum in a few experiments.

McCann and MacGinitie (1965), studying visual acuity in insects, stress the importance of great precision with regard to the manufacture of stimulus patterns, and demonstrate how noisy patterns can give erroneous results due to the animal responding to subharmonics present in the stimulus. However, the experiments described in this thesis were not concerned with acuity and so inaccuracies in the drum, though certainly present, were of little importance.

The drum was illuminated from above by a 60W pearl bulb shining through a diffusing screen. Drum illumination could be altered at will, by changing the voltage to this lamp. All stripes appeared evenly illuminated by this method.

The drum was driven by a reversible electric motor giving a smooth drive at a wide variety of different velocities. Drive smoothness at low velocity was tested by a flag and photocell method essentially similar to that used for recording eye movements. No irregulaties could be detected in the movement, and no vibration was transferred from the electric motor to either the drum or the crab.

Drum movement was monitored in different ways in different experiments. When the drum was rotated continuously, its movement was monitored directly by a linear potentiometer geared directly to the drum spindle. Potential changes were displayed on the pen recorder alongside the eye movement records. In memory experiments, where the drum is moved in the dark through a known angle, and in experiments where $1/2^{\circ}$ to 2° step and ramp stimuli were used, an arm attached to the outside of the drum moved between two stops a known distance apart. When the arm was not touching either step, a circuit was broken which caused the time trace of the pen recorder to be interrupted. In this way the time taken for the drum to move through a known angle was ascertained.

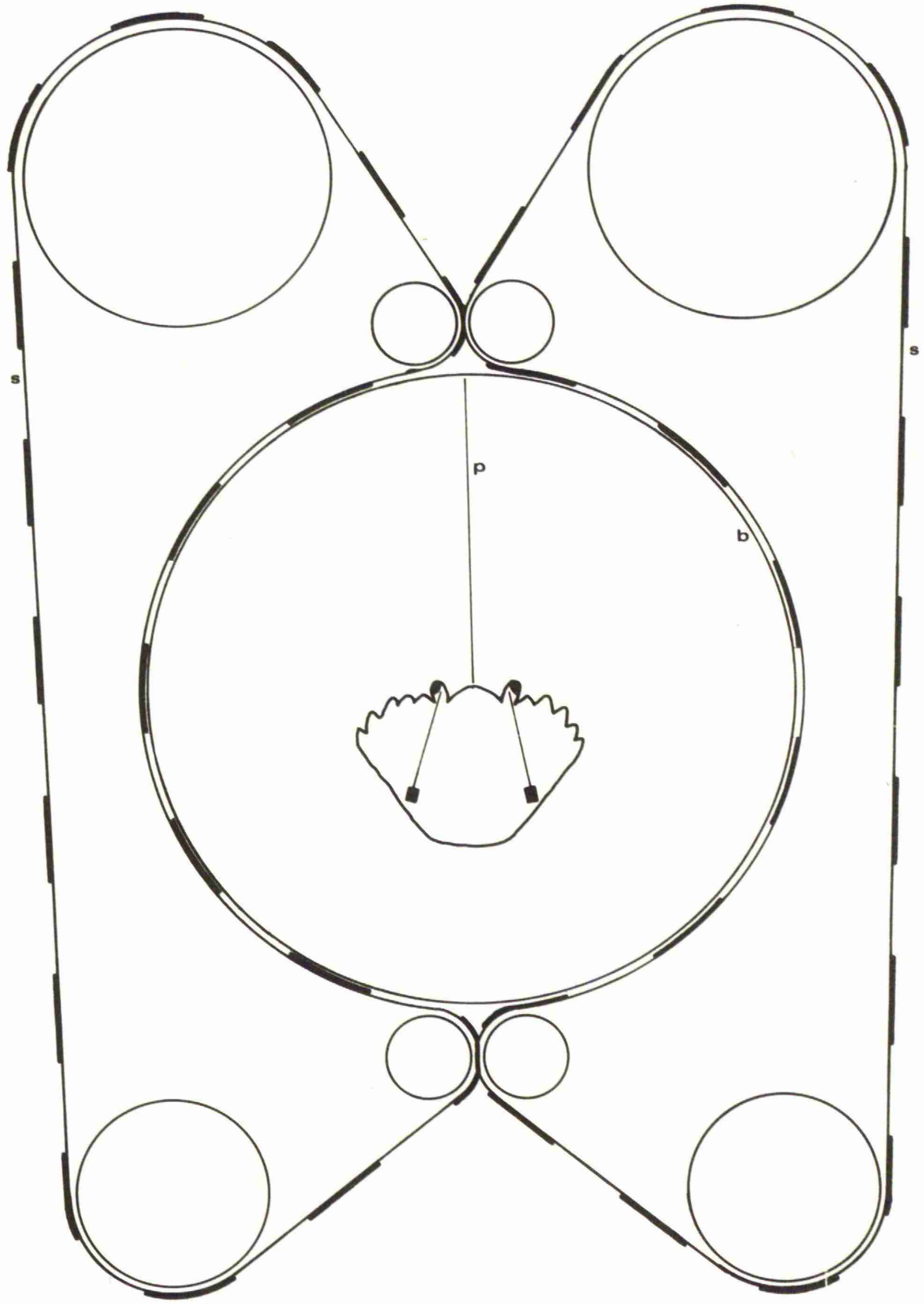
A device was also designed that enabled the eyes of crabs to see different visual fields (Fig. 8.). A crab was clamped in the centre of a large glass bowl around which two loops of stripes could be revolved in either direction at a variety of different velocities. The stripes were driven by reversible multispeed motors and monitored by potentiometers in a similar way to a normal drum. In some experiments a partition was placed between the eyes of the crab so that neither eye could see the stripes on the opposite side of the drum. However, removing the partition did not change the responses in any way so, for convenience, it was left out in most experiments.

The responses of crabs to the movements and apparent movements of small lights was also studied. These experiments were carried out in a light-proof room, where the only light was the minute stimulus bulb of a few milliwatts. The crab always faced the stimulus which was c.50 cms away from it and on the same level. The stimulus used was a subminiature bulb (1.5V, 45 mA Pinlight, Kay Electric Co., Fairfield, New Jersey) which gave an illumination at the crab's eye of about 0.05 lux (Horridge, 1966d).

In some experiments, one or more pinlights were rotated in a circle in front of the crab; in others, ramp stimuli were used. For these latter experiments, the pinlight was mounted on the end of a light arm of a pen recorder solenoid (Southern Instruments Ltd., pen unit type M940B) driven by a low frequency waveform generator (Servomex, type

FIGURE 2.

Arrangement enabling the two eyes of a crab to have different visual stimuli. The crab was clamped in the centre of a 14 ins. diameter glass bowl (b), around which 2 loops of stripes (s) could be revolved in either direction at a variety of different velocities. The partition (p) was present in only a few experiments; its absence did not affect the results in any way. Photocells and clamp holding crab were left out of diagram for simplicity.


s
s
p
b

LF51). This provided linear movement over small distances with considerable accuracy and a frequency response of up to 10 c.p.s.

For apparent motion stimuli, a series of equally spaced pinlights was switched on and off in a variety of different sequences giving the illusion of movement, the moment of switching being registered on the pen recorder used to record the eye movements.

RESULTS

1) NORMAL EYE MOVEMENTS

In the absence of moving stimuli, the eyes of crabs are by no means stationary but exhibit a variety of oscillations over a wide frequency spectrum. The movements can be conveniently classified into four categories: tremor, drift, flicks or saccades and scanning movements.

Tremor

Tremor in the horizontal plane of amplitude 0.01° - 0.2° and frequency 1-3c.p.s. was first observed in the eyes of crabs by Horridge & Sandeman (1964), and further studied by Horridge (1966f), who also noted tremor in the vertical plane.

When eye movements were plotted in two dimensions on an X-Y plotter, tremor could be seen to occur in all planes (Fig. 3). With a stationary pinlight in an otherwise dark visual field, eye drift was reduced and tremor occurred continuously in more or less the same place. Because of this, two dimensional records of tremor alone were difficult to analyse, but close examination of plots such as Fig. 3A, showed that tremor in the horizontal plane predominated over tremor in other planes.

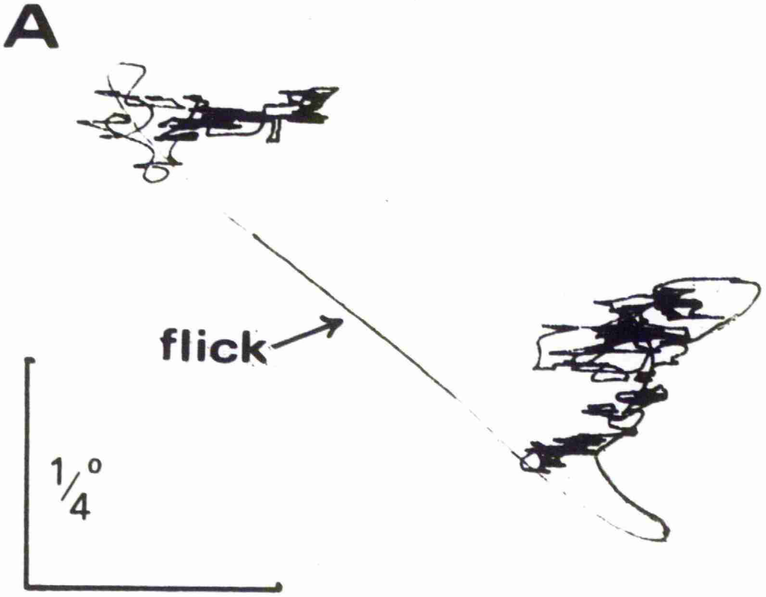
Tremor was more clearly observed during the response of the eye to a moving pinlight as shown in Fig. 3B. Analysis of such records confirmed that tremor, far from being a simple sinusoidal movement, was

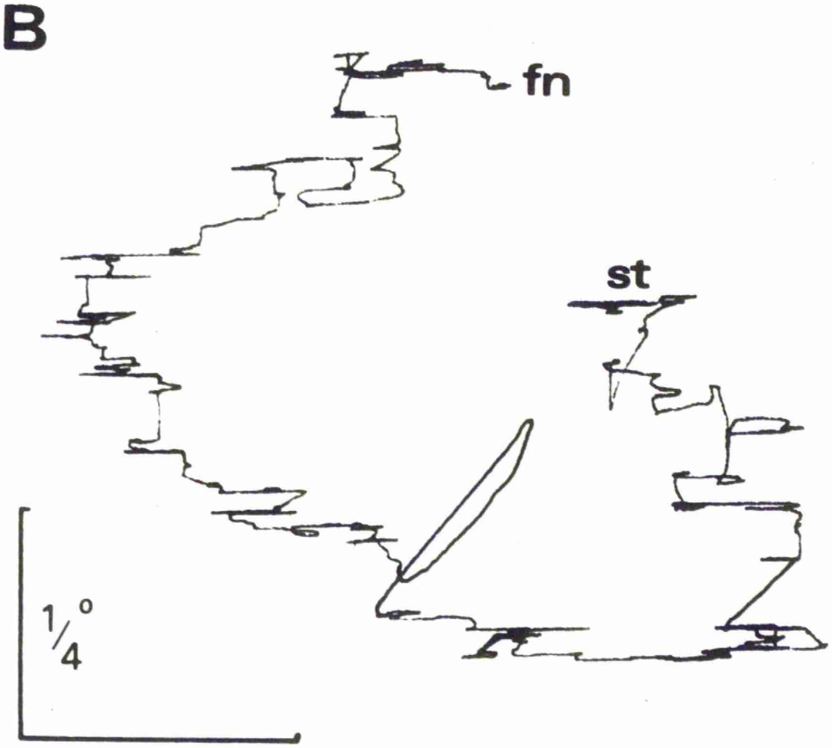
FIGURE 3.

Two-dimensional records of eye tremor.

A. Tremor over a period of 40 seconds with eye partially stabilized by a stationary pinlight. Note that flick occurred after about 20 seconds.

B. Tremor occurring during a response to a pinlight moved in a clockwise circle from a 12 o'clock position. The cycle took 48 seconds, the stimulus diameter subtending 2.7° at the crab's eye. st = start. fn = finish.


A
flick
1/4°


B
fn
st
1/4°

a complex irregular movement of several superimposed oscillations in different planes, and contained frequencies of up to 10 c.p.s. The dominant motion was in the horizontal plane and all measurements of tremor frequency and amplitude were measurements of this dominant oscillation. Though tremor amplitude could be easily calculated and is 0.01°-0.1° peak to peak in Fig. 3B, it was impossible to measure tremor frequency with any accuracy. This was due to the absence of a time scale on two dimensional plots of eye responses. However rough estimations were made, the mean frequency of tremor being 1-2 c.p.s. in Fig. 3B.

Accurate measurements of tremor frequency and amplitude in the horizontal plane were obtained from one dimensional records of eye movement. Examination of a large number of such records from different crabs showed that large variations occurred in both tremor amplitude and frequency. All values were, however, within the range 0.01°-0.2° peak to peak and frequency 1-3 c.p.s.

Horridge & Sandeman (1964) suggested that a visual field of contrasting stripes reduced the eye tremor amplitude that occurred with a plain white visual field. Repetition of this experiment failed to confirm this result, but did demonstrate that contrasting objects in the visual field reduced the low frequency components of eye movement which are defined below as drift. Measurements of tremor amplitude under different ambient light intensities have given different results in different crabs. Three of the five animals studied failed to show any change in tremor, while the other two showed a reduction of tremor amplitude in the dark of 10-30%. This is a much lower figure than that obtained by Burrows (personal communication), who has observed tremor reductions of over 50% when the lights are turned out.

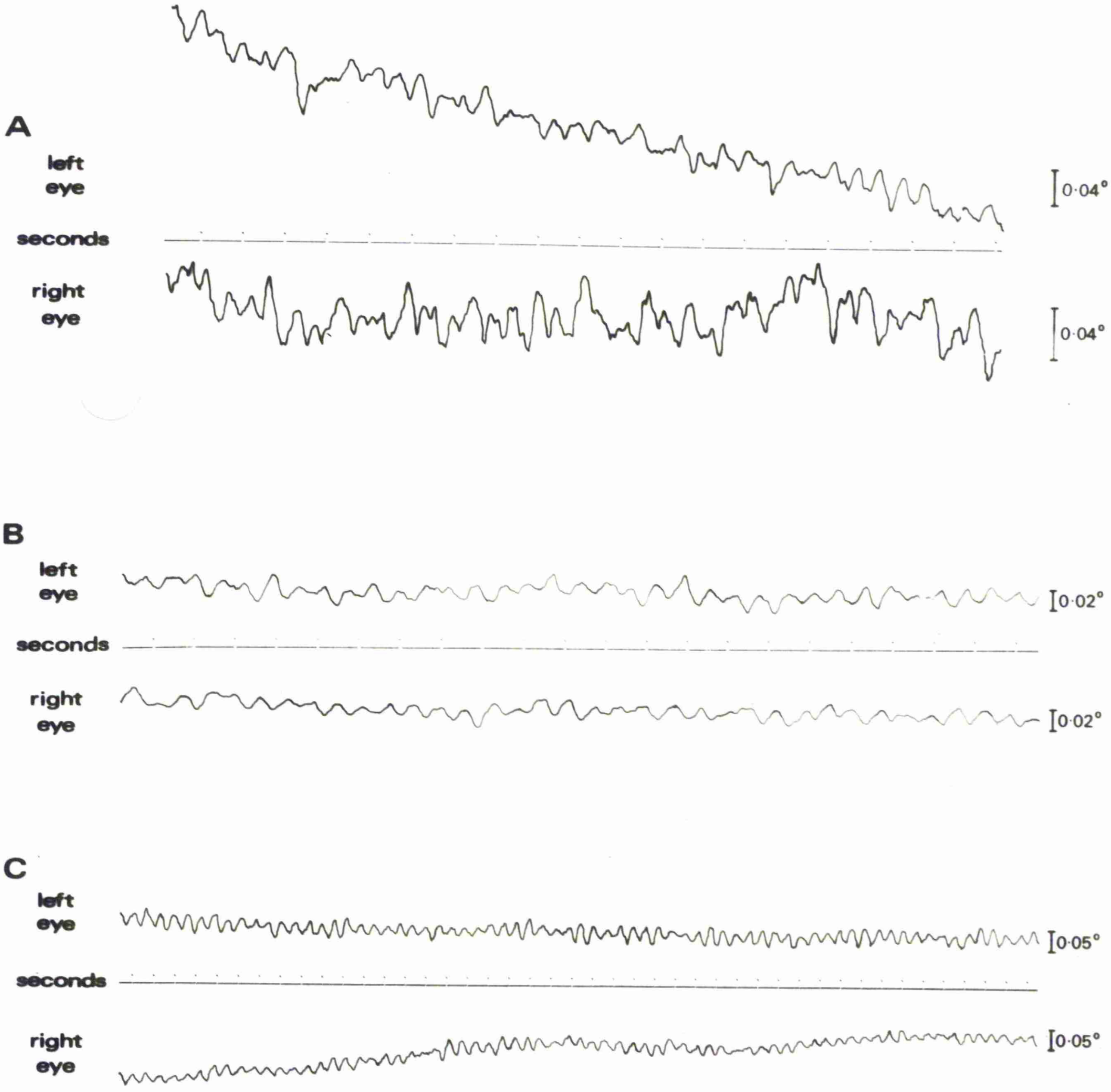
During optokinetic responses to the movement of a striped drum, changes in tremor amplitude and frequency were often observed. These changes were greatest when the direction of the optokinetic response of the eye changed, and at the start of an optokinetic response when tremor amplitude was often increased. Tremor frequency and amplitude also seemed to depend on the position of the eye in its traverse, though little consistency was found between one crab and another in this respect.

Though the evidence of these experiments is by no means conclusive, they give weight to the theory that eye tremor is not just 'noise', but is under the control of the central nervous system and can be modified to some extent by external factors such as light intensity changes and moving stimuli. Indeed, Burrows (personal communication) has obtained good correlation between the phasic activity of muscles 20a and 21 and the dominant oscillation of eye tremor.

When the movements of both eyes were recorded simultaneously, the eyes of most crabs oscillated quite independently of each other (Fig. 4A). However, in two of the crabs examined, the tremors of the two eyes were closely linked. In one (Fig. 4B), both eyes oscillated at 1.6-1.8c.p.s. and 0.01° - 0.02° peak to peak, 180° out of phase with each other. In

FIGURE 4.

Eye tremor from both eyes of three different crabs. A. Normal situation with the two eyes independent of each other. Note drift of left eye. B. Unusual situation where the tremors of the two eyes were 180° out of phase with each other. C. Unusual situation where the tremors of the two eyes were exactly in phase. Movement to the right is shown by a downwards movement of the trace.


A
left eye
seconds
right eye
0·04°
0·04°
B
left eye
seconds
right eye
0·02°
0·02°
C
left eye
seconds
right eye
0·05°
0·05°

the other (Fig. 4C), the eyes were in phase, tremor being 1.7-1.8c.p.s. and 0.03° - 0.06° peak to peak. In both these crabs the linkage observed between the eyes was maintained for all of the three to four hours that the crabs were observed. Though such a close linkage is undoubtedly an unusual phenomenon for which no explanation can be given, the fact that it occurred shows that, in some crabs at least, tremor is under central control.

Drift

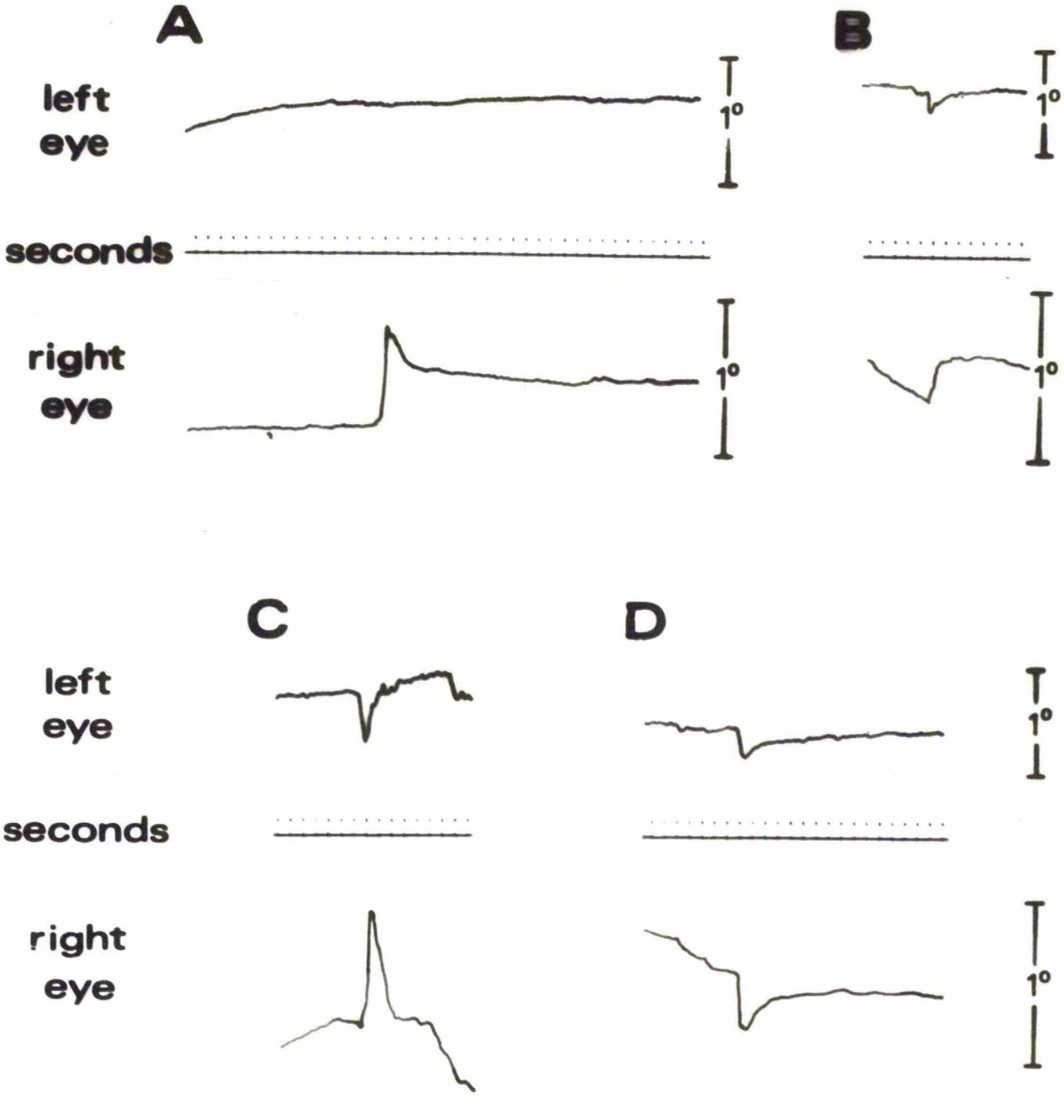
Slow, usually irregular, wandering eye movements are defined as drift. Drift is particularly prevalent when the eye sees no contrasts in its visual field, and is reduced by optokinetic stabilization when contrasting objects are present (Horridge, 1966f). The present work has shown that drift, like tremor, occurred in all planes and that it affected the two eyes independently (Fig. 4A). Its velocity seldom exceeded 0.01°/sec.

Flicks or saccades

The spontaneous jumps that occur irregularly every few minutes in eye movement records were described as saccadic flicks by Horridge (1966f). That there was usually a subsequent return towards the previous position of the eye, and that this occurred even in blinded eyes (Fig. 5A), suggested that flicks are imposed independently by a distinct neuron bearing an occasional burst of impulses. Two dimensional plots showed that flicks occurred in all directions (Fig. 3A),

FIGURE 5.

Eye flicks from two different crabs (B, C, & D same crab). In all records the right eye has been blinded. A. Towards midline 0.7° flick and partial return by blinded right eye. B. Towards midline 0.25° flick and partial return by seeing left eye; apparently this was interpreted as a drum movement by the blinded eye, which responded by moving the same distance in the opposite direction 0.5 secs later. C. As B, but larger movements. D. Both eyes flicked simultaneously to the right and partially returned towards their former positions.


A
B
left eye
1°
1°
seconds
right eye
1°
1°
C
D
left eye
1°
seconds
right eye
1°

and records from two eyes simultaneously demonstrated that flicks sometimes, though by no means always, occurred in both eyes together (Fig. 5). Their frequency and amplitude were extremely variable. Flicks are thus very similar to partial retraction reflexes, which appear as flicks occurring away from the crab's midline in response to stimuli such as touch and changes in light intensity.

Scanning movements

The scanning movements described by Horridge & Sandeman (1964) in *Carcinus* appear to be partial retraction reflexes and have, therefore, not been classed as a distinct group of eye movements.

However, eye scanning does occur in *Carcinus* and was always associated with a period of leg waving. It occurred predominantly in the horizontal plane (Fig. 6A) and independently in the two eyes (Fig. 6B), at an amplitude of 0.1° - 2.0° peak to peak and frequency 2-3 c.p.s. Its visual significance has not been assessed.

Also associated with leg waving is an increase in the gain of optokinetic responses. These were first described by Horridge (1966f) and were confirmed in the present studies. Sandeman (personal communication) has observed eye scanning without leg movement in the crab *Pachygrapsus*.

FIGURE 6.

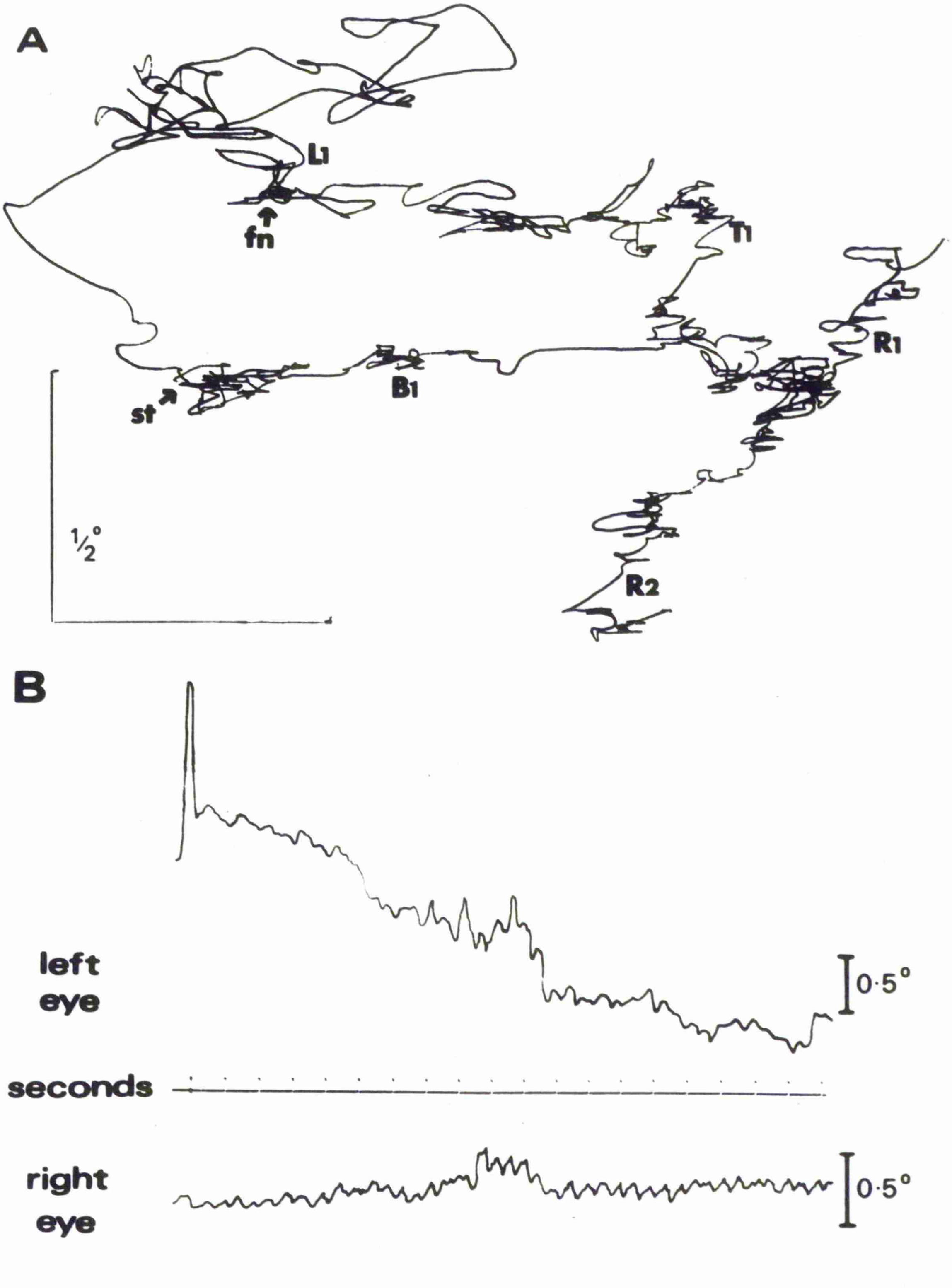
Eye scanning correlated with leg waving.

A. Two-dimensional record of eye scanning occurring during response to a pinlight moved in a 40 sec clockwise circle whose diameter subtended 9° at the crab's eye.

st. start of eye scanning; fn. its termination;

R1, B1, L1, T1 and R2 are 3 o'clock, 6 o'clock, 9 o'clock, 12 o'clock and 3 o'clock second time around positions of pinlight respectively.

B. Eye scanning recorded from both eyes simultaneously. Note lack of synchronization between the eyes, amplitude varying between 0.1° and 1° and frequency of about 2 c.p.s. Movement to the right is shown by a downwards movement of the trace.


A
L1
fn
T1
R1
st
B1
R2
1/2°
B
left eye
0·5°
seconds
right eye
0·5°

2) GENERAL ASPECTS OF OPTOKINETIC RESPONSES

Optokinetic nystagmus in Carcinus consists of two phases, a slow forward phase during which the eyes follow the direction of rotation of the environment around the animal, and a fast return phase in which the eyes are flicked back in the opposite direction. The response is most easily obtained by rotating a vertically black and white striped drum, the stripes subtending an angle of 10° - 30° at the crab's eye, around the crab at a velocity between 0.01° and 10°/sec. Fig. 7 illustrates the slow and fast phases of the response and demonstrates that when the direction of the drum movement was changed, nystagmus occurred over a different part of the eye's traverse. The full extent of the eye traverse differed in different crabs from 20° - 40°, with a norm of 25° - 30°, while fast phase amplitudes usually varied between 8° and 15°.

The slow phase

Considering only the slow following phase of the optokinetic response, it can be seen from Fig. 7, and is illustrated graphically in Fig. 8A, that the eye moves more slowly than the drum. The stimulus which elicits the optokinetic response is the movement of the stripes across the retina. Now, as the ommatidia are on the effector organ, the eyecup, the response necessarily reduces the stimulus, so that the effective stimulus to the ommatidia is the difference between the eye speed and the drum speed; this is termed the slip speed. As can be seen from Fig. 8A, the response is much greater than the effective stimulus. This demonstrates the presence of an amplifier in the eye

FIGURE 7.

Record of optokinetic responses from both eyes simultaneously, produced by rotation of a vertically black and white striped drum around the crab. Note that the full extent of the eye traverse (25° in this crab) was much greater than the extent of the fast phases (5° - 15°). Movement to the right is shown by a downwards movement of the trace.

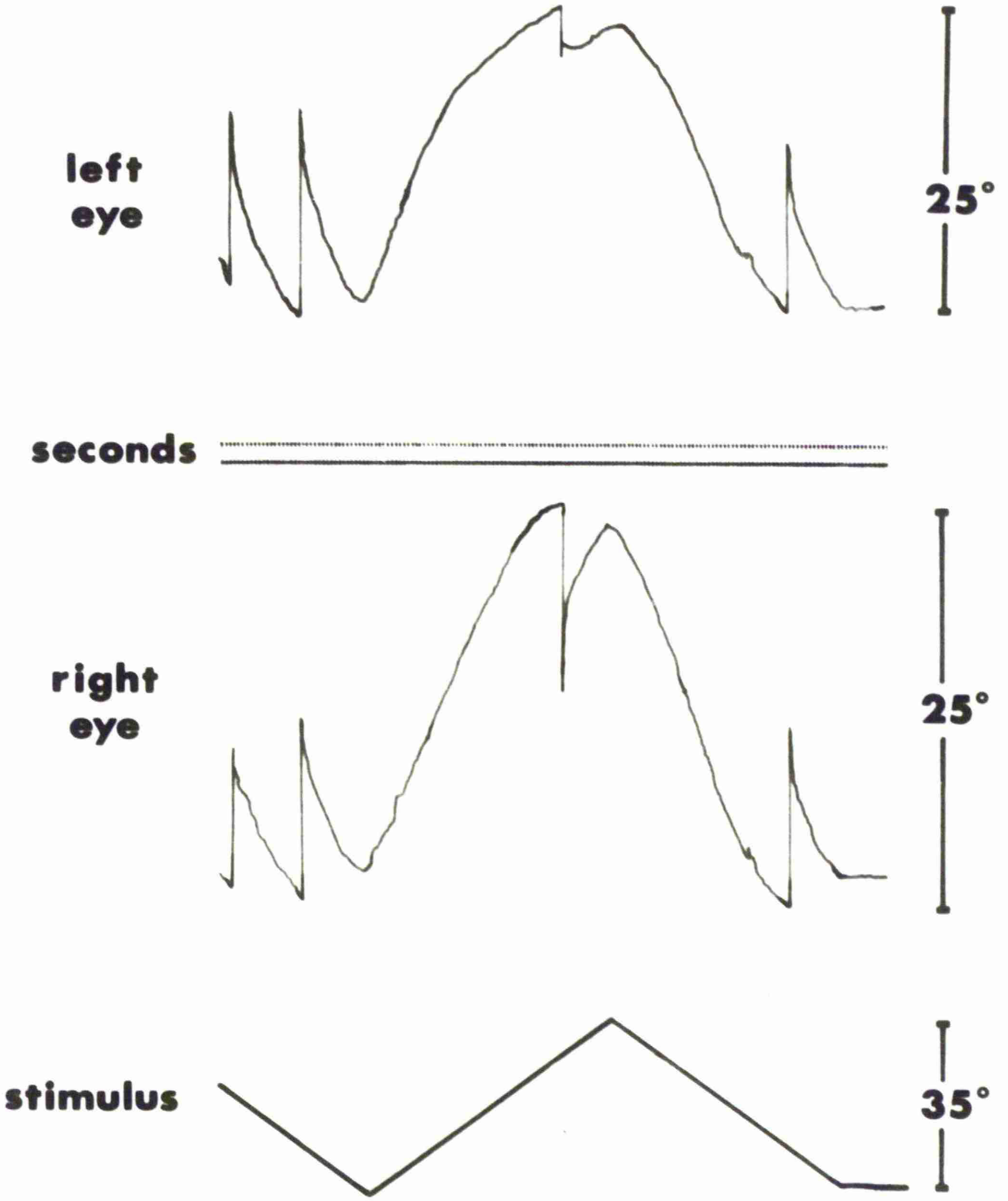

left eye
25°
seconds
right eye
25°
stimulus
35°

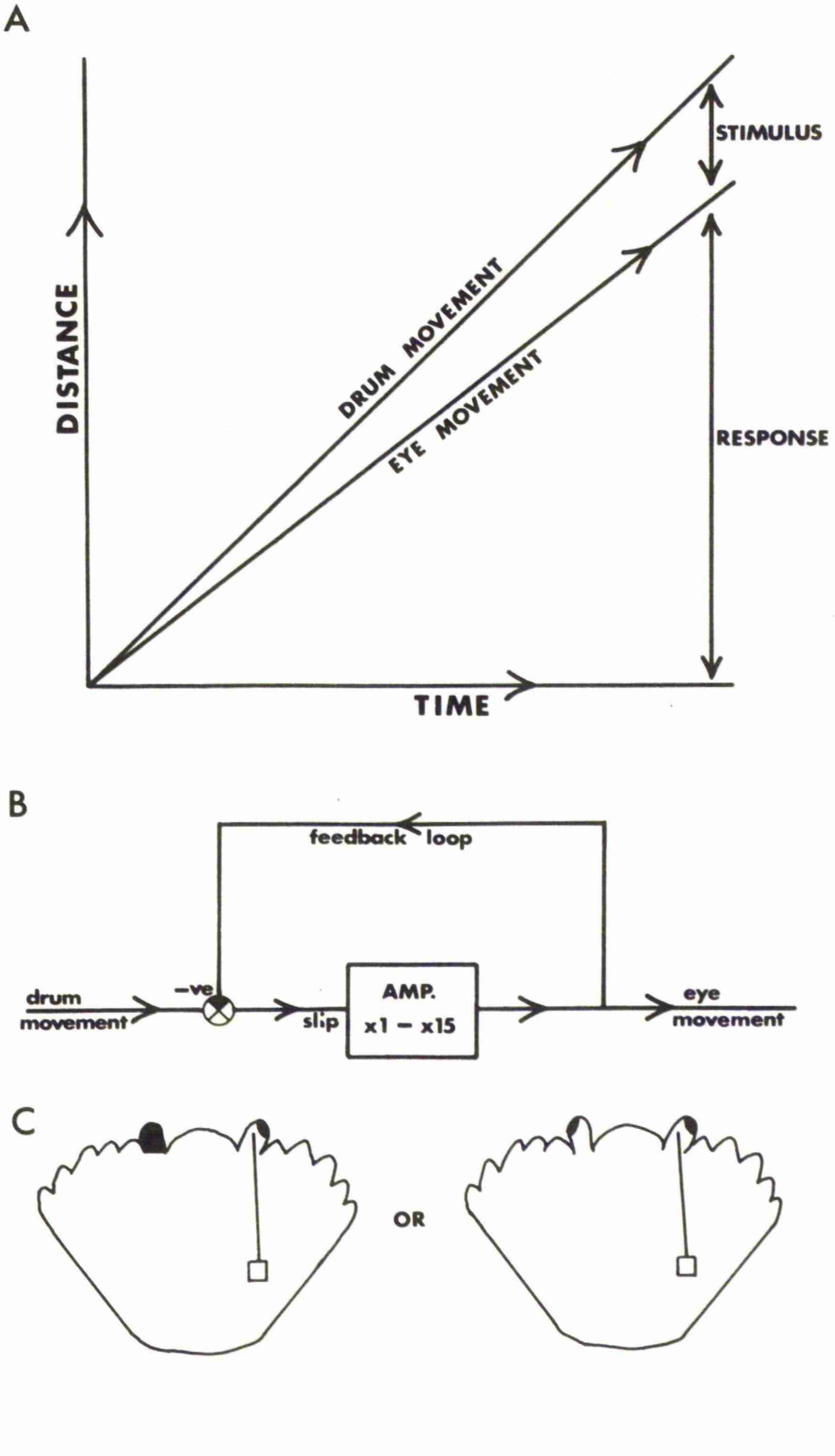
FIGURE 8.

The slow following phase of optokinetic nystagmus, normal closed loop condition.

As shown in the graph (A), the eye moves more slowly than the drum. As explained in the text, the response necessarily cuts down the stimulus, so that the actual stimulus to the eye is the drum movement minus the eye movement. The graph illustrates that the response is much larger than the stimulus to the eye, confirming the presence of an amplifier in the eye movement control system.

The control system is more exactly represented by the block diagram (B). The input is the drum movement; from this is subtracted the eye movement, via the negative feedback loop, to give the slip speed. This is amplified up to fifteen times by the eye movement control system amplifier, so that the resultant output, the eye movement, is up to fifteen times the actual movement seen by the crab.

This system applies to the responses of seeing eyes of unilaterally blinded crabs or to either of the eyes of crabs seeing the same visual stimulus with both eyes (C).


A
DISTANCE
DRUM MOVEMENT
EYE MOVEMENT
STIMULUS
RESPONSE
TIME
B
feedback loop
drum movement
-ve
slip
AMP.
x1 – x15
eye movement
C
OR

movement control system. The gain (gain = $\frac{\underline{\text{output}}}{\text{input}}$) of this amplifier changes with stimulus velocity (Horridge & Sandeman, 1964) and even shows small variations at constant stimulus velocity. However, experiments in which the eye responses were measured with the eyes in different positions have shown that, except at the extreme eye positions, the gain of the amplifier does not depend on the position of the eye. There is no fovea in Carcinus and no fixation of any kind by the eye; different regions of the eye are thus exactly equivalent to each other.

The eye movement control system is more conveniently represented by the block diagram Fig. 8B. The input to the system is the actual stimulus, the drum movement. From this is subtracted the eye movement via the negative feedback loop, so that the input to the eye movement control system amplifier is the slip speed which equals the drum speed minus the eye speed. This is amplified up to fifteen times so that the resultant eye velocity is up to fifteen times the effective velocity seen by the ommatidia. This system, representing the unilateral closed loop condition, was described by Horridge (1966g), and is the system which applies to experiments conducted on the responses of the seeing eyes of unilaterally blinded crabs, or either of the eyes of crabs seeing the same visual stimulus with both eyes (Fig. 8C), for, in this latter condition, bilateral effects are very small.

When the visual feedback loop is broken, the situation is termed open loop. This may be achieved by recording isometrically the force exerted by the seeing eye of a crab blinded in one eye, but in these experiments was accomplished by recording the movements of a blinded eye, with the other eye seeing but fixed to the carapace (Fig. 9C). This latter method was considered preferable, since results obtained by the former method would be in terms of the force exerted by the eye and thus not directly comparable to closed loop experiments. In this, the open loop 'through brain' condition, the input to the eye movement control system is the drum movement (Fig. 9B), so the resultant eye velocity is up to fifteen times the drum velocity (Fig. 9A).

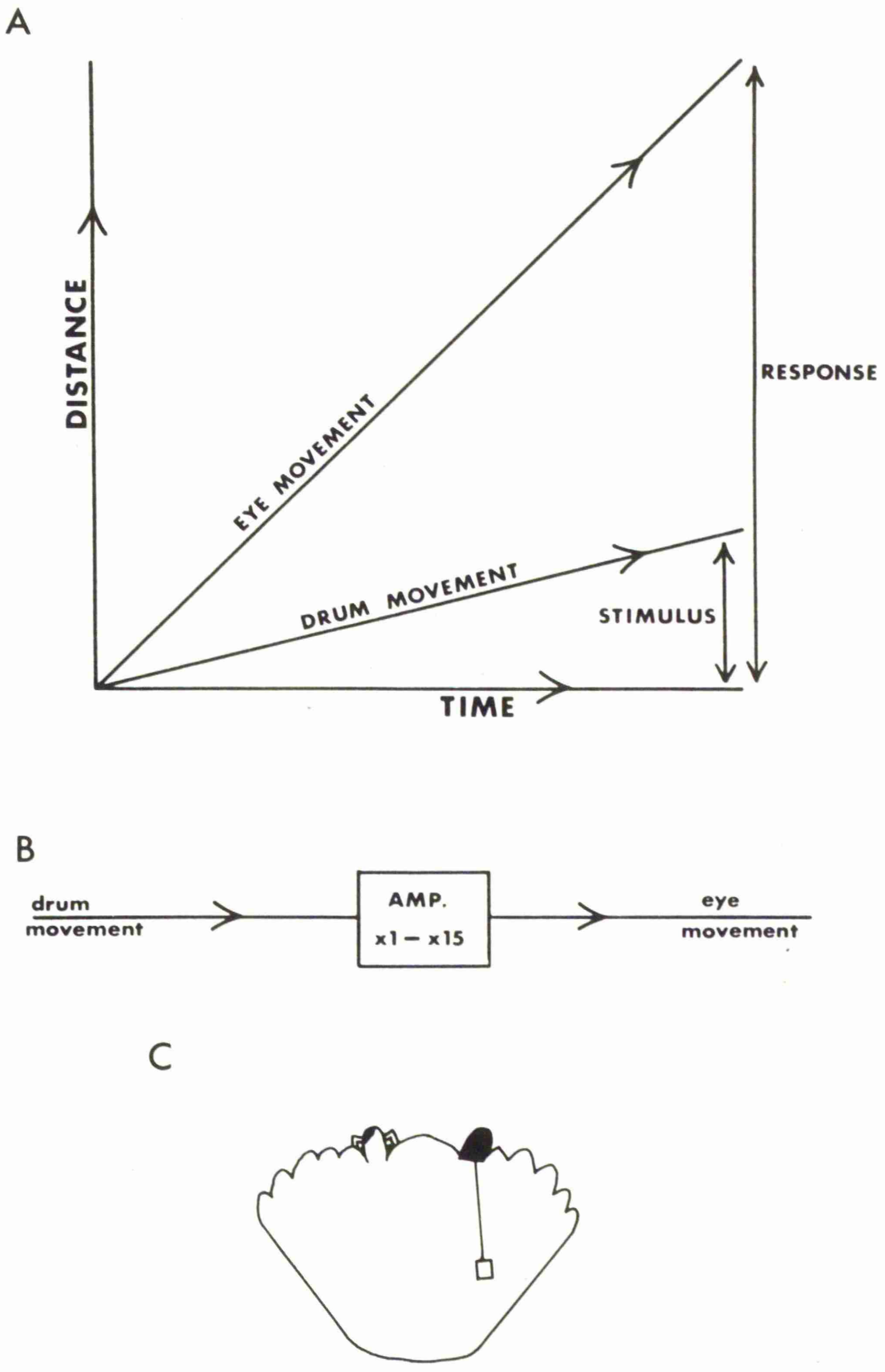
The control system described so far with only a visual feedback loop does not enable a crab to distinguish between apparent movement produced by rotation of the eye and image movement resulting from the displacement of objects in the external world. If crabs can make such a distinction, they must either have a proprioceptive feedback loop, or a 'reafference' system as described by von Holst and Mittelstaedt (1950). In such a 'reafference' system, the crab would have a central mechanism which anticipates the visual change which ensues when the animal initiates its own movement. The crab could achieve this by monitoring the oculomotor output to its eye muscles. This anticipated visual change or 'efferent copy' would neutralise the resultant reafferent visual information induced by turning and the animal would perceive a stationary environment.

The eye sockets of Carcinus contain many hairs, most or all of which can reasonably be presumed to be mechanoreceptors. The crab thus has proprioceptive information concerning eye position available for the

FIGURE 9.

The slow following phase of optokinetic nystagmus, open loop condition.

When visual feedback is prevented, the eye moves much faster than the drum (A). The block diagram (B) represents this open loop condition, which is achieved by recording the movements of a blinded eye with the seeing eye fixed to the carapace (C).


A
DISTANCE
EYE MOVEMENT
DRUM MOVEMENT
STIMULUS
RESPONSE
TIME
B
drum movement
AMP.
x1 — x15
eye movement
C

formation of a proprioceptive feedback loop for the control of eye movements. However, examination of the movements of both eyes of crabs blinded in one eye demonstrated that flicks occurring spontaneously in the seeing eye were often closely followed by a movement in the opposite direction by the blinded eye (Fig. 5B,C). As the movements of the two eyes did not occur simultaneously (the seeing eye always flicked first) and the movements occurred both towards and away from the crab's midline, these movements could not have been partial retraction reflexes. Instead it appeared that the central nervous system interpreted the flick as a movement of the environment by an equal amount in the opposite direction, the blinded eye responding accordingly by a movement in the opposite direction to that of the flick. This demonstrates that any afferent information from possible proprioceptors present in the eye sockets of Carcinus is not used for the control of eye movements.

Two observations by Horridge and Sandeman (1964) confirm the above view - that there is no proprioceptive feedback loop for the control of eye movements in Carcinus. Firstly, they forcibly moved the seeing eye of an unilaterally blinded crab with a fine probe, and observed that the blinded eye responded as if the environment had moved by an equal amount in the opposite direction, i.e. the blinded eye moved in the opposite direction to the imposed movement of the seeing eye. When this experiment was repeated after blinding the seeing eye, there was no response from the other eye. Secondly, they noted that unilaterally blinded crabs, with the oculomotor nerve to the seeing eye transected, showed normal optokinetic responses from the blinded eye, even though the seeing eye necessarily remained stationary.

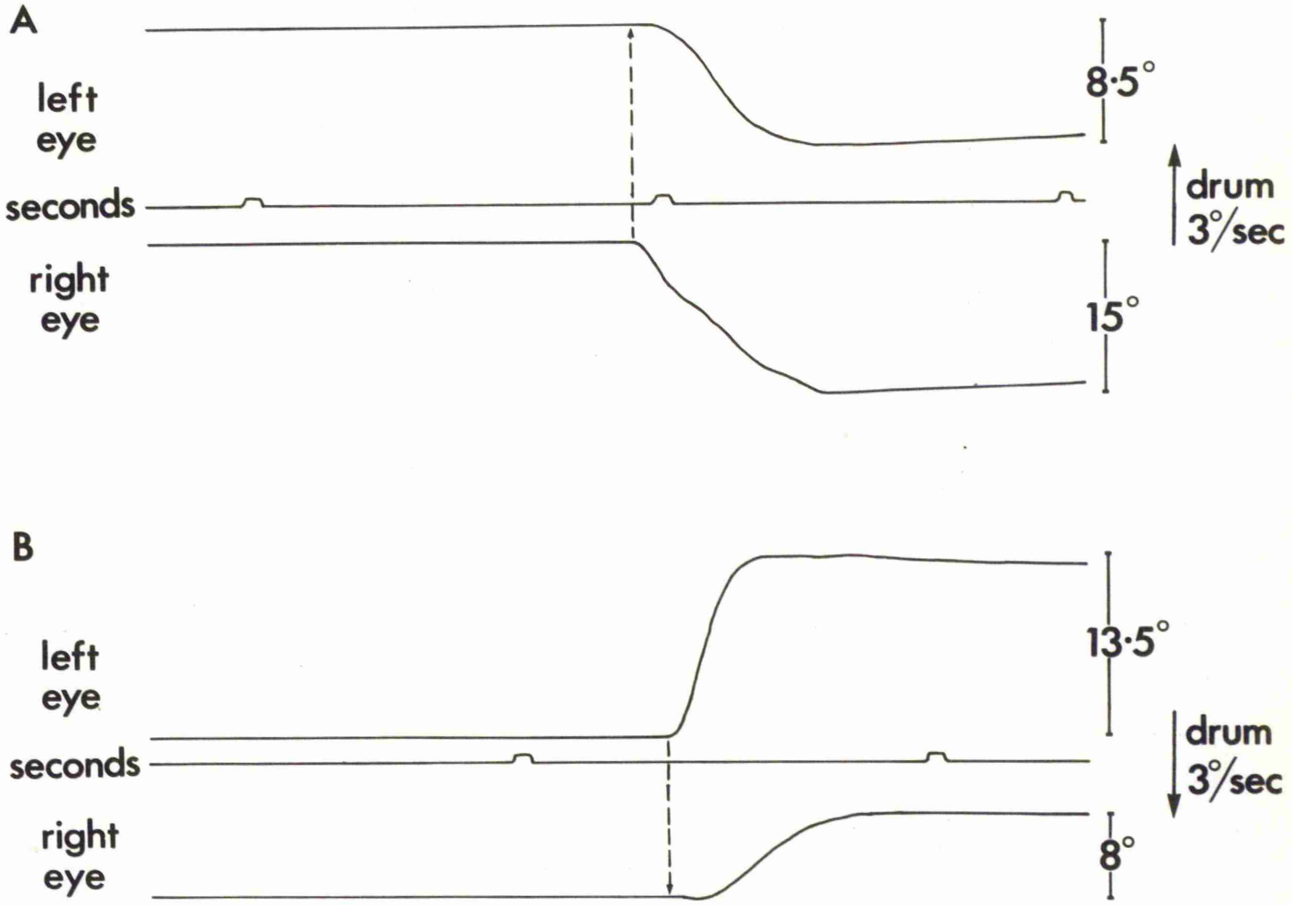
This leaves the possibility of a 'reafference' system. Though such a system undoubtedly exists in man, the experimental evidence put forward for reafference in crustacean visual systems can also be interpreted in terms of visual feedback. In fact, the result of the spontaneous saccade experiment described above suggests that reafference is not a property of the visual system of *Carcinus*, for the movement of the retinal image, caused by the saccade, induced an optokinetic response in the blinded eye (Fig. 5B,C). Also, as will be discussed later, almost all the optokinetic responses of *Carcinus* seem to be 'designed' to stabilise as far as possible the image of the environment on the ommatidia and hence to minimise the need for a 'reafference' system. It may thus be that *Carcinus* is unable to distinguish between apparent movement induced by itself and actual movement of the environment.

The fast phase

The fast phase of optokinetic nystagmus is illustrated in Fig. 10, and is a fast return of the eye to its starting position in the opposite direction to the rotation of the environment. The response, which takes 200-500 msecs is usually a smooth movement, though small, jerky fast phases are sometimes observed in fatigued crabs. Fig. 10A illustrates

FIGURE 10.

Fast phases of optokinetic nystagmus from both eyes simultaneously. A. Drum moved to left; note that right eye led left eye and moved through a larger angle. B. Drum moved to right; left eye led and moved further.


A
left eye
8·5°
seconds
drum 3°/sec
right eye
15°
B
left eye
13·5°
seconds
drum 3°/sec
right eye
8°

that, for drum movement to the left, the fast phase of the right eye led that of the left eye by 30-80 msec. When the drum was moved to the right, the fast phase of the left eye led by a similar amount. The significance of this will be discussed when the initiation of the fast phase is considered in detail (Section 7). It can also be seen from Figs 7 and 10 that fast phases occurring away from the midline of the crab were usually of greater magnitude than those occurring in the opposite direction.

3) RESPONSES TO LIGHTS

In this and the following sections, different aspects of the crab's optokinetic responses, discussed in general in the last section, will be considered in detail.

Although in almost all measurements of the optokinetic response, both in vertebrates and invertebrates, the stimulus of preference has been the striped drum, a single moving light is in many ways a much more convenient stimulus. A single light can be arranged to move vertically as well as horizontally or in a circular path, thus introducing a second dimension to the stimulus that is impossible with the striped drum. Also, instead of actual movement taking place, the stimulus can be an apparent movement initiated by switching on one or more lights at the instant that one or more other lights are switched off. Many other experiments, such as using light of different wavelengths or polarizations are also possible but have not been explored in the present work. Moreover, the use of a single light overcomes several of the disadvantages of striped drums. The most important of these is that striped drums are difficult to manufacture without subharmonics which arise from uneven illumination or faults in the stripes; and even in experiments where the presence of subharmonics is unimportant, it is equally difficult to manufacture other drums with exactly the same specification. The presence of upper and lower edges on a drum, and the impossibility of centring both eyes of a crab within a drum are also disadvantages eliminated by the use of small lights as optokinetic stimuli. The only other workers to have used a point source of light as an optokinetic stimulus were Ter Braak (1936), Rademaker and Ter Braak (1948) on the dog and the rabbit, and Horridge (1966d) working with _Carcinus._ In the following experiments, which are in many ways an extension of those of Horridge (1966d), the eye responses of _Carcinus_ to the movement of small lights were recorded in two dimensions, which had not been done previously. The responses to the apparent movement of pinlights and the responses to interacting movements of lights and stripes were also studied.

Two dimensional recordings of responses to moving pinlights

Horridge has shown that the eyes of _Carcinus_ exhibit following optokinetic responses to vertical movements of a horizontally black and white striped drum (Horridge, 1966f) and to horizontal movements of a pinlight in an otherwise dark room (Horridge, 1966e). In order to examine in detail the responses of the eye to pinlights moved vertically as well as horizontally, eye movements were recorded in two dimensions as described earlier. Two dimensional recording had the advantage that it enabled a visual representation of the movement of the eye in space to be achieved. However, these X-Y plots of eye responses did not enable the velocity of the eye to be calculated with any degree of accuracy. In most experiments crabs were used in the closed loop condition with both eyes seeing.

Circular stimuli.

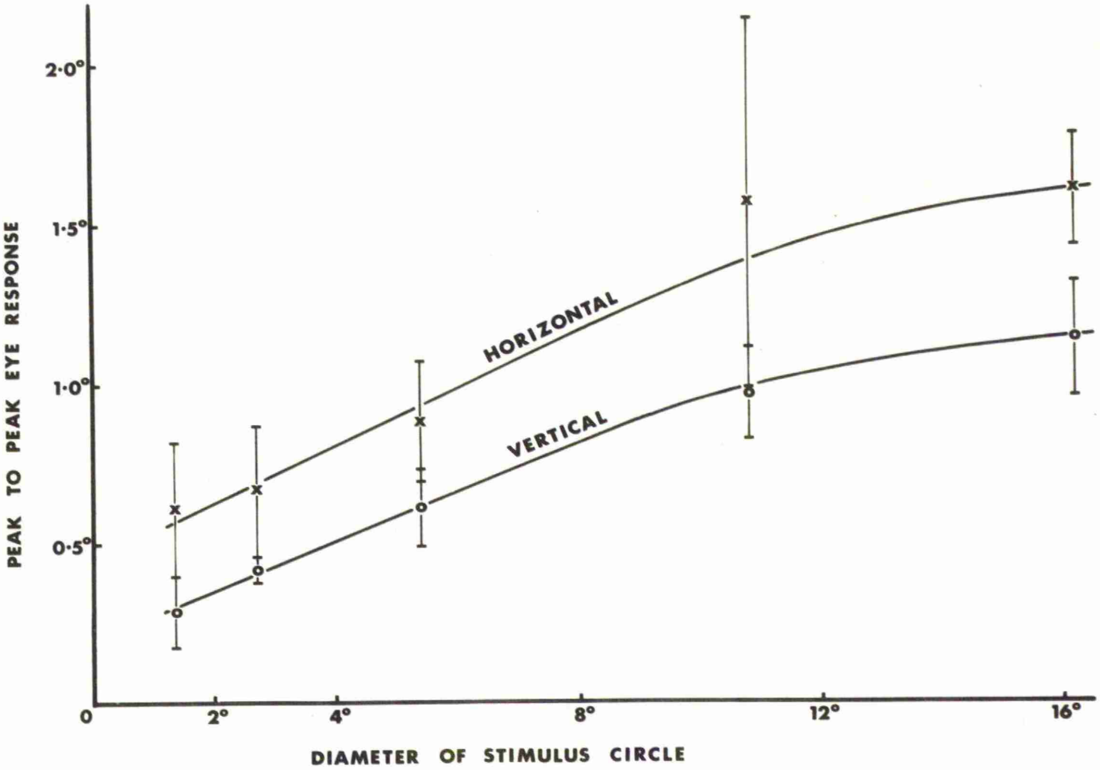
The movement of a pinlight in a circle in front of the crab was a simple stimulus incorporating both vertical and horizontal movement. There were no other contrasting objects in the visual field, the room being uniformly dark except for the pinlight. The result of such an experiment is shown in Fig. 3B. Though the eye response was by no means an exact circle, the eye certainly responded to the circular stimulus, demonstrating that vertical movement and movement at different angles between horizontal and vertical are just as easily elicited from the eye as horizontal movement. Eye tremor and in this instance a small eye flick were superimposed on the response.

Unlike the stimulus of a moving striped drum to which all crabs respond optokinetically, only one-third of the crabs used in these experiments responded to the movements of pinlights having an intensity of 0.05 lux at the crab's eyes. The crabs that did not respond to the movement of pinlights appeared in no other way different from those that did. It is thus concluded that the movement of a point source of light of low intensity is an optokinetic stimulus to which only the crabs with the most highly developed optokinetic responses can respond. The small size of all responses to moving lights, compared with those to moving stripes, to some extent confirms this conclusion.

Changes in the size of the circle subtended at the eye by the moving pinlight caused corresponding changes in the response of the eye. In Fig. 11, the peak to peak horizontal and vertical movements of the eye were measured for each completed circle of the stimulating pinlight, and plotted against the diameter of the stimulus subtended at the eye. The

FIGURE 11.

Horizontal and vertical peak to peak eye responses to the movement of a pinlight in a clockwise circle in front of the crab. Stimulus frequency - 48 secs/cycle; amplitude varying. X - axis - diameter of circle subtended at eye by pinlight. Y - axis - horizontal and vertical diameters of the more or less elliptical paths of the crab's eye in response to the moving pinlight. Vertical lines represent standard deviations from the mean of between 4 and 13 responses. The curves representing the average horizontal and vertical responses of the eye were drawn by hand to fit as many experimental points as possible.


2·0°
1·5°
1·0°
0·5°
PEAK TO PEAK EYE RESPONSE
0
2°
4°
8°
12°
16°
DIAMETER OF STIMULUS CIRCLE
HORIZONTAL
VERTICAL

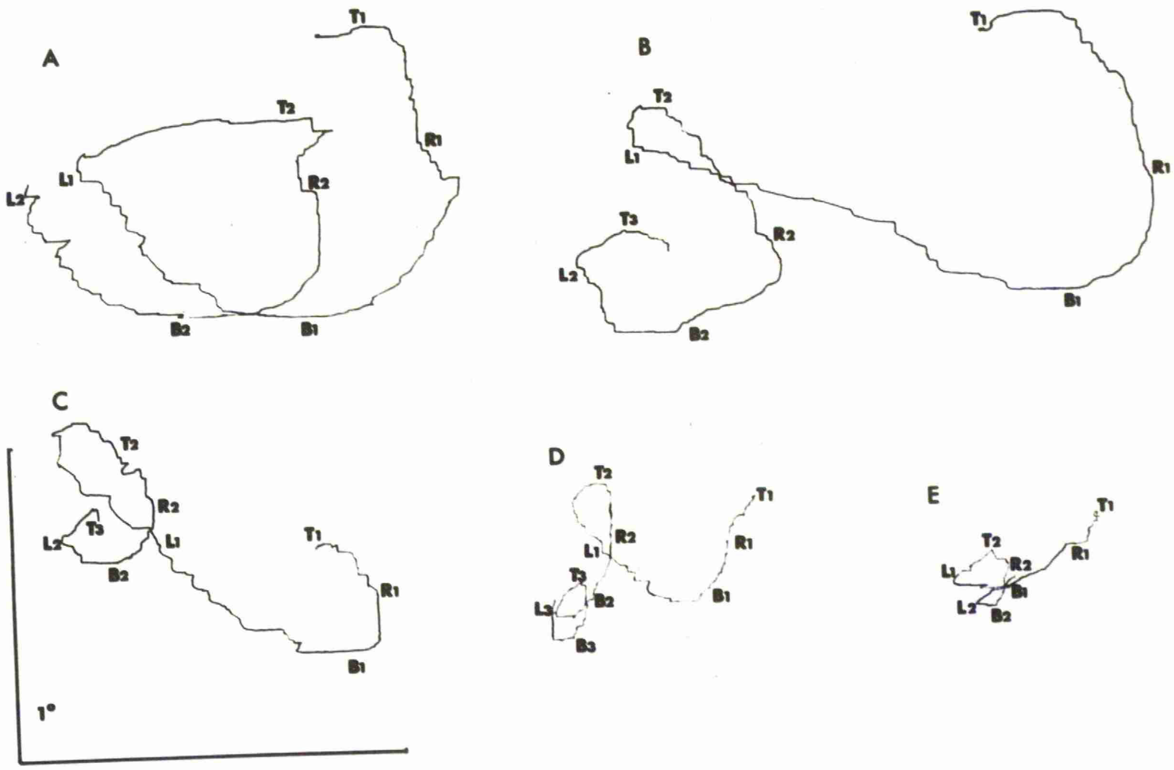
results plotted on the graph were all from the same crab, though similar results were obtained on other specimens. The graph shows that the horizontal extent of the eye movement was consistently greater than the vertical one, i.e. the responses were approximately elliptical. The vertical extent of the response to a 2° diameter circle was 18% of the stimulus diameter, while the horizontal response was 30%. When the stimulus was an 8° diameter circle, the responses had dropped to 10% and 14% respectively. These responses may be compared to the 50-90% responses that would be given to the movement of a striped drum at similar velocities through similar angles. The vertical lines on the graph represent standard deviations from means of between four and thirteen individual responses; they demonstrate the considerable variability of all crab's responses to the movement of pinlights. The mean responses to increasing the stimulus diameter, frequency remaining constant, from a 2° diameter circle to a 10° - 12° diameter circle increased approximately linearly. This linear increase, however, was not maintained for stimulus diameters above 12°.

The effect of changing the frequency of a stimulus circle of constant amplitude is illustrated in Fig. 12. At frequencies between 30 and 200 secs / cycle, the only changes observed were slight increases in the sizes of the responses with decreasing frequency. This is due to the increase in the velocity gain of the control system amplifier at low frequencies (Horridge & Sandeman, 1964; Horridge, 1966d). At increasing frequencies from 30 secs/cycle to 10 secs/cycle, the horizontal extent of the response to the first circle or part of circle

FIGURE 12.

Two-dimensional records of the eye responses to a pinlight moved in a clockwise circle from a 12 o'clock position; stimulus amplitude constant, frequency varying.

The stimulus diameter subtended 18.6° at the crab's eye. A. 41 secs/cycle. B. 27.5 secs/cycle. C. 20 secs/cycle. D. 15 secs/cycle. E. 10.5 secs/cycle. T1, R1, B1 and L1 are, respectively, the 12 o'clock, 3 o'clock, 6 o'clock and 9 o'clock positions of the pinlight during the first cycle. T2, R2, B2 and L2 are similar positions for the second cycle etc. Note lower initial gains and greater adaptation at higher frequencies.


A
T1
T2
R1
R2
L1
L2
B2
B1
B
T1
T2
L1
R1
T3
R2
L2
B1
B2
C
T2
R2
T3
L2
L1
B2
T1
R1
B1
1°
D
T2
T1
L1
R2
R1
T3
B2
L3
B1
B3
E
T1
T2
R2
L1
R1
B1
L2
B2

decreased from 7% to 2% of the stimulus diameter. As well as this decrease, however, there was considerable adaptation of the response after the first 1/2-1 circle had been completed for all frequencies greater than 30 secs/cycle. This often led to a spiral response rather than the usual circular or elliptical response (Fig. 12B, C, D and E). The adaptation was never to zero, however, the response still persisting even after many cycles of stimulation. A similar adaptation of the optokinetic response was observed to high frequency sinusoidal oscillation of a striped drum by Horridge (1966f).

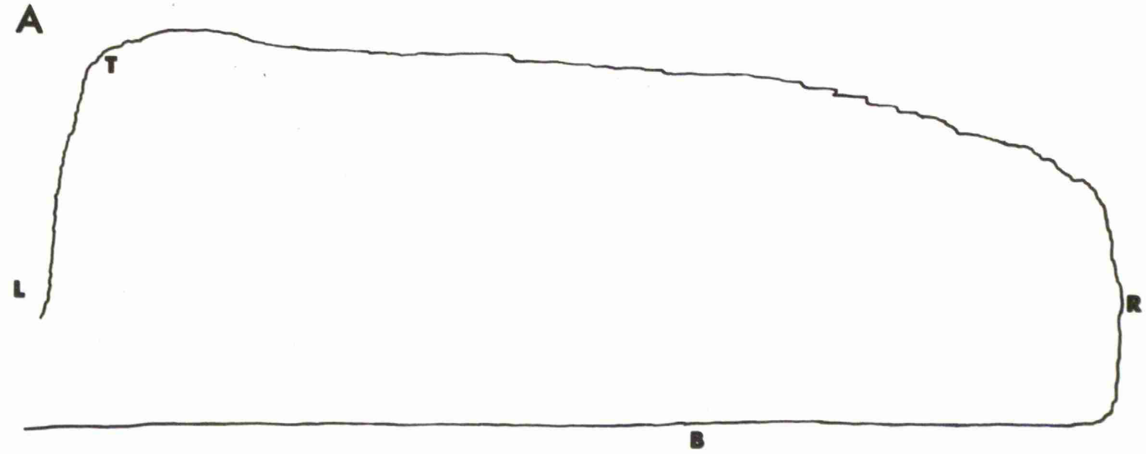
Though the response of most crabs to the slow movement of a pinlight in a circle was either an approximate circle or ellipse, two of the many crabs studied gave almost square responses to this stimulus (Fig. 13A). In order to analyse these responses further, the pen of the X-Y plotter was intermittently lifted from the paper by a make and break circuit driven by a metronome. This enabled the time spent by the eye on the different parts of the 'square' to be observed directly. The results from these records (Fig. 13B) were inconclusive showing only that the movement of the eye was rather irregular, speeding up and slowing down at different points in different circles. Certainly this experiment gave no insight into the mechanism by which a crab responded to a circle by reproducing a square.

However, these 'square' responses may only be an extreme example of a very common phenomenon, for there were indications in many records of the crab's responses to the movement of a pinlight that diagonal

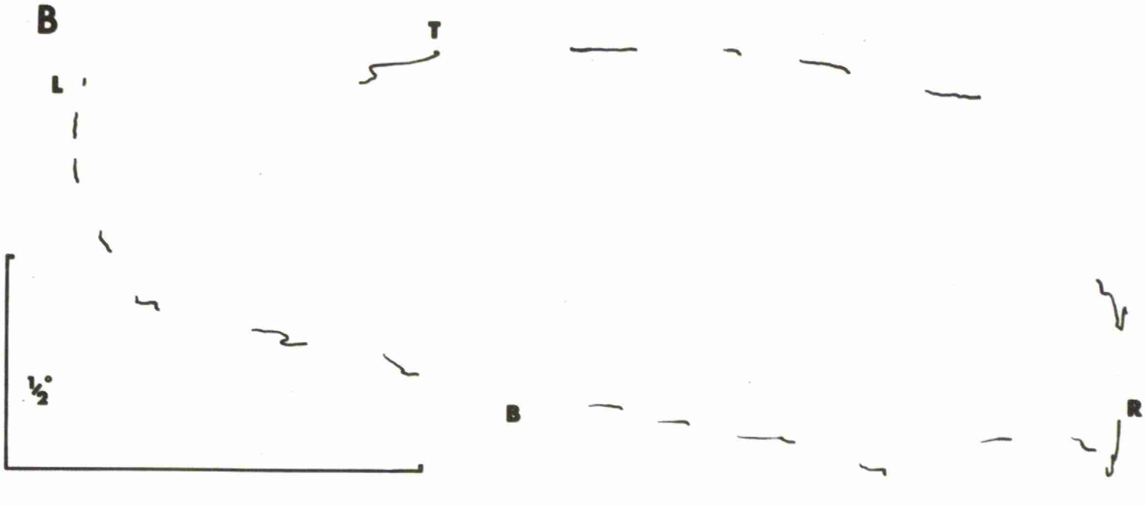
FIGURE 13.

Two-dimensional records of the almost square responses occasionally given by the crab's eyes to the movement of a pinlight in a circle in front of the crab. Stimulus diameter subtends 18.6° at crab's eye, stimulus frequency - 60 secs per cycle. T., R., B. and L. are the 12 o'clock, 3 o'clock, 6 o'clock and 9 o'clock positions of the pinlight respectively. In B, the pen of the X-Y plotter was intermittently lifted (dash + space = 2½ secs), so that the time spent by the eye at different points on the "square" could be observed.

A



B



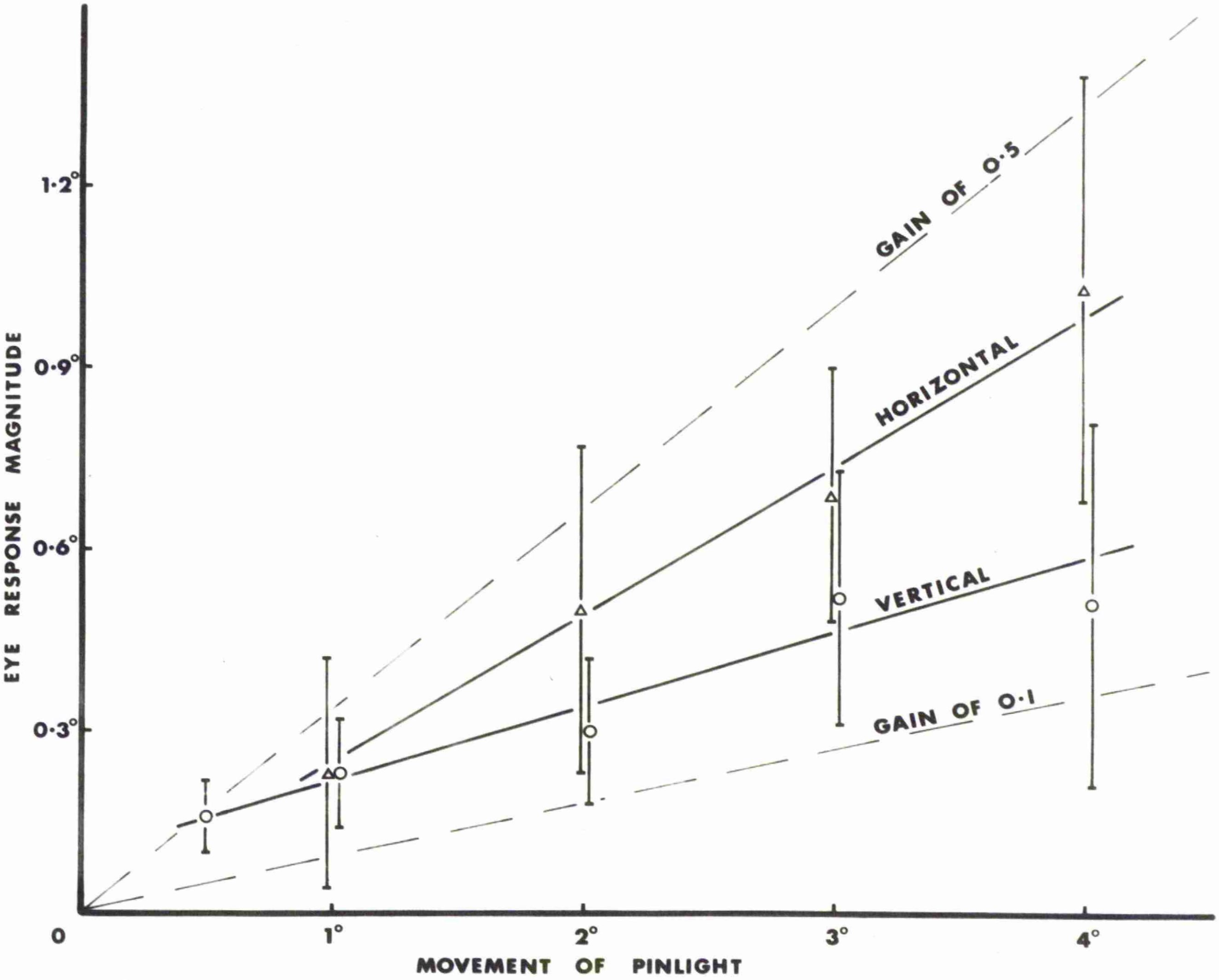
movements were achieved by a stepwise movement (e.g. Fig. 12A,B,C,D). The extent of the alternating horizontal and vertical movements that composed this 'staircase' was usually 0.05° - 0.1°. The 'steps' were probably the result of rather coarse interaction between the different muscles of the eye, for it is difficult for the central nervous system to produce a smooth diagonal movement when most of the eye muscles act in either the vertical or the horizontal plane. There are, however, two other possible explanations for this phenomenon. It may simply represent eye tremor superimposed on a pure diagonal movement, or reflect an analysis, possibly in the optic lamina, of all movements into their horizontal and vertical components. This last possibility is considered later when the ability of crabs to respond to ramp stimuli at different angles to the horizontal is considered with respect to the possible use of these optokinetic responses in orientation and navigation.

Ramp stimuli.

Although some measure of the linearity of the vertical and horizontal eye responses to the movement of pinlights was shown in Fig. 11, changing the amplitude of a circle of constant frequency results in consequent changes in the velocity of movement of the light. A better measure of the linearity of these responses was therefore achieved by using ramp stimuli of different amplitudes but constant velocity. Fig. 14 shows the results of two such experiments on the same crab. In

FIGURE 14.

Responses to constant velocity horizontal (△) and vertical (O) ramp movements of a pinlight in front of the crab. Velocity of stimulus - 0.1°/sec. X - axis - amplitude of ramp stimulus. Y - axis - amplitudes of eye movement. Vertical lines represent standard deviations from the mean of between 4 and 14 responses. Straight lines representing the average responses of the eye were drawn by hand to fit as many experimental points as possible. Theoretical lines representing gains of 0.5 and 0.1 are drawn on the graph for comparison with the responses.


EYE RESPONSE MAGNITUDE
1·2°
0·9°
0·6°
0·3°
0
1°
2°
3°
4°
MOVEMENT OF PINLIGHT
GAIN OF 0·5
HORIZONTAL
VERTICAL
GAIN OF 0·1

one the ramp stimuli were in the vertical plane, in the other the horizontal plane. Similar results were obtained from other animals. The variability of the responses was considerable and their gain low, being in the horizontal plane 0.3, equivalent to responses of 25% of the stimulus, and in the vertical plane 0.2-0.3, equivalent to responses of 15-25% of the stimulus. In this, the closed loop condition, the gain (G) of the eye movement control system was calculated from the equation -

$$G = \frac{R}{S - R}$$

where R = eye response,

and S = stimulus magnitude.

The results were similar to those obtained by moving a pinlight in a circle but much smaller than those obtained by moving a multistriped drum around the crab (Horridge & Sandeman, 1964). In responses to the movement of drums of stripe repeat distance 10-30° there is considerable spatial summation of signals from many pairs or small groups of receptors from many different parts of the eye (Thorson, 1966a). When the stimulus is the movement of a pinlight, summation can only occur to a small extent as a pinlight stimulates far fewer receptors than does a multistriped drum. The low gain of these responses was thus not unexpected. Though Horridge (1966d) gives 1° as the limit for linearity for the eye responses of crabs to the movement of pinlights, Fig. 14 shows that, both for horizontal and vertical responses, reasonable linearity was maintained for stimuli between the limits of 1° and 4°.

No fast phases were observed to horizontal movements of pinlights though the low gain of these responses suggests that their absence was not in any way fundamental.

Open loop responses

Ramp movements of pinlights were also used as stimuli for crabs in the open loop condition (one eye blind and free to move, the other eye seeing but fixed). However, whereas one third of crabs responded to the movement of a pinlight when in the closed loop condition, only two crabs, out of a total of more than twenty tried (i.e. $<10\%$), responded when in the open loop condition. One of these crabs was also among the few to respond under open loop conditions to the movement of a single black-white edge. As there is no reason to suppose that the absence of visual feedback affects the ability of crabs to respond to the movement of single edges or pinlights, the low number responding to these stimuli is probably due to the prevention of eye tremor in the seeing eyes of crabs in the open loop condition.

Though the form of the open loop response of these two crabs did not differ from the closed loop responses, the gains of responses to both horizontal and vertical ramps were extremely variable. However, this was not unexpected, for it is a property of negative feedback loops to decrease response variability. The mean gains for the responses of these two crabs were of the same order of magnitude as those occurring under closed loop conditions and were as follows.

Crab A - mean horizontal gain = 0.5 at ramp velocity 0.4°/sec.
mean vertical gain = 0.15 at ramp velocity 0.4°/sec.

Crab B - mean horizontal gain = 0.15 at ramp velocity 0.03°/sec
decreasing to 0.002 at ramp velocity 0.3°/sec.

Orientation.

Ramp movements of pinlights were further used to analyse the ability of Carcinus to measure the angle of movement of a light, a necessary prerequisite for orientation or navigation.

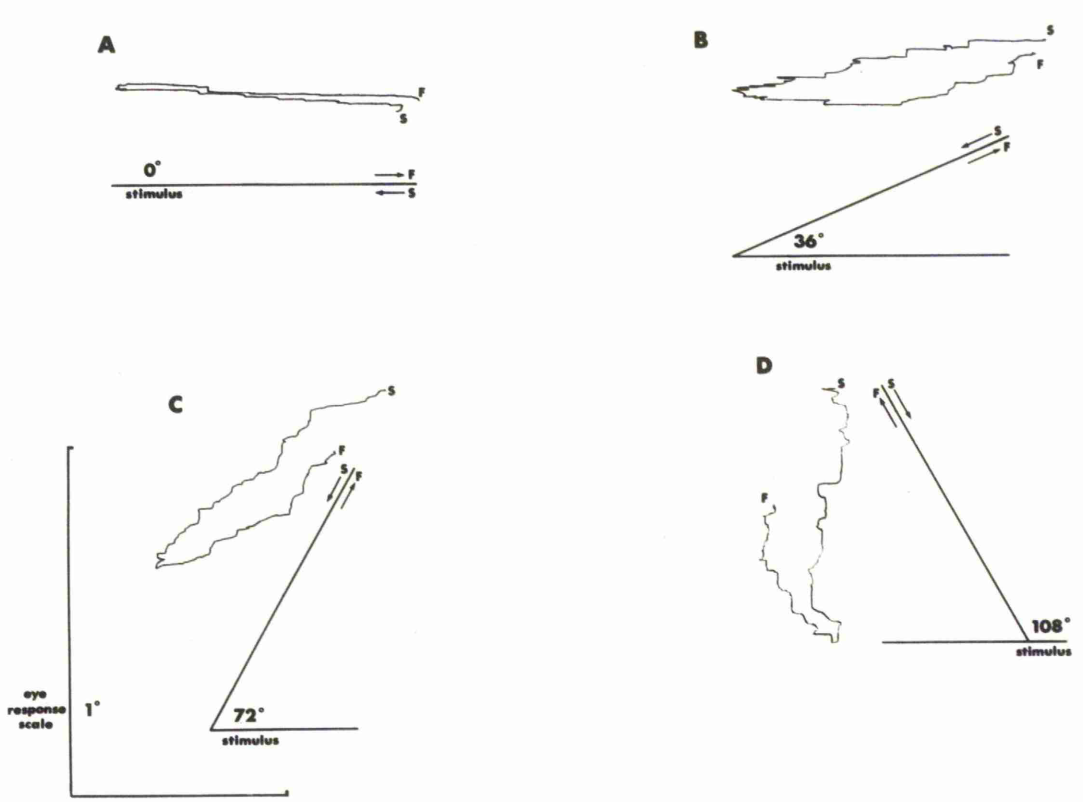
Horridge (1965, 1966e) has shown that Carcinus responds optokinetically to the movement of the sun across the sky in the absence of other contrasting objects in the visual field. Whether the direction of the sun or moon is used for orientation or navigation is, however, unknown. Pardi and Papi (1961) have shown that the littoral amphipods Talitrus and Talorchestia can navigate correctly towards or away from the sea in the absence of any landmarks except the sun, the direction of the sun at different times of the day being taken into account by reference to an internal 'clock'. The only published work on Carcinus is by Drzewina (1908) who found that Carcinus released on a beach headed towards water. Though she called this reaction a hydrotropism, it seems much more likely that it was either a direct orientation towards shadows as described by Alverdes (1930) for Carcinus, or some mechanism such as that described above for Talitrus and Talorchestia. More recently, work by van Tets (1956), quoted by Pardi and Papi (1961), suggests that the Pacific shore crab <u>Hemigrapsus</u>, seeing only the sun and the sky, usually orientates itself parallel to the waterline of the beach from which it was taken. This reaction did not occur on overcast days.

All this evidence points to some navigational ability in <u>Carcinus</u>. For crude navigation, orientation with respect to the sun's azimuth is enough; for a more highly developed sense, the sun's altitude must also be taken into account. In order to test the ability of <u>Carcinus</u> to measure such movements, a pinlight stimulus, as already described, was moved in front of the crab at constant velocity at different angles to the horizontal. The responses shown in Fig. 15 were to a pinlight moved at 1°/sec, though repetition of the experiment with a stimulus velocity of 0.005°/sec (the same order of magnitude as the speed of the sun across the sky) gave similar results. The function of these optokinetic responses in orientation is hard to assess and it may be that they are just a by-product of the perception of the direction and velocity of movement of the sun.

It is noteworthy that the diagonal responses of Fig. 15, like the diagonal components of the responses to a pinlight moved in a circle, were achieved by a stepwise movement. Though, as discussed earlier, this may simply be superimposed eye tremor or the result of rather coarse interaction between the horizontal and vertical muscles of the eye, it may mean that diagonal movements are resolved into their horizontal and

FIGURE 15.

Two-dimensional records of responses to ramp movements of a pinlight in front of the crab at different angles to the horizontal. Stimulus angles subtended 5° at crab's eye; start (s) to finish (f) time was 10 secs; i.e. ramp velocity - 1°/sec. As the vertical and horizontal eye response scales are unequal, a response of e.g. 36° would make an angle of $23\frac{1}{2}^{\circ}$ with the horizontal. The diagrams representing the stimuli, drawn adjacent to each eye response, are adjusted to allow for this discrepancy.


A
F
S
0°
stimulus
F
S
B
S
F
S
F
36°
stimulus
C
S
F
S
F
eye response scale
1°
72°
stimulus
D
S
F
S
F
108°
stimulus

vertical components. Though such a computation is not strictly necessary for a sun compass response, it is necessary for homing responses such as those occurring in birds released in an unknown direction from their homes. This resolution of movement into horizontal and vertical components could occur in the lamina or even in the more posterior neuropiles, for all are orientated with strict reference to the horizontal and vertical axes of the animal in its normal posture (Horridge, 1966e).

Theoretically, if such a resolution occurs, then the angles of the responses of Fig. 15 should be dependent upon the relative gains of the responses to horizontal and vertical stimuli. Fig. 16 gives different theoretical response curves for different ratios of vertical:horizontal gains. If the gains for vertical and horizontal responses are equal, then the angle of the responses given by the crab should equal the stimulus angles for all angles. However, if the horizontal and vertical gains are unequal, as in Fig. 14, then a graph of stimulus angle against response angle will not be a straight line, but will be a curve, stimulus angle only equalling response angle at 0°, 90° and 180°. Graphs of two such experiments are shown in Figs. 17 and 18.

When the individual responses from which the graph, Fig. 17, was drawn were resolved into their horizontal and vertical components, and the mean horizontal and vertical gains were calculated, the following values were obtained:

mean horizontal gain = 0.3

mean vertical gain = 0.2

FIGURE 16.

Theoretical curves for the angle of eye movement in response to ramp stimuli at different angles to the horizontal. The different curves represent expected responses if the vertical : horizontal gain ratio ($\frac{V}{H}$) had the values 0, 0.1, 0.2, ...2.5.

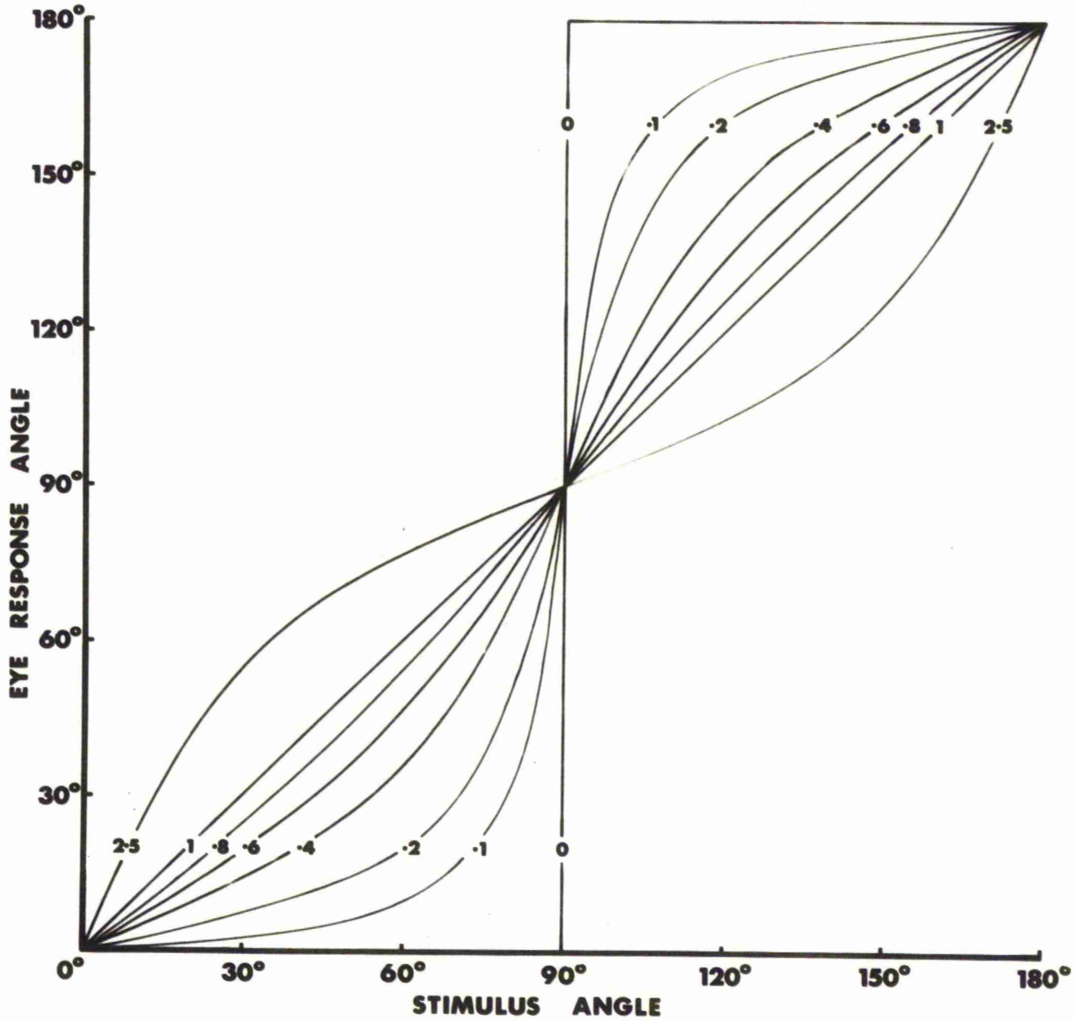
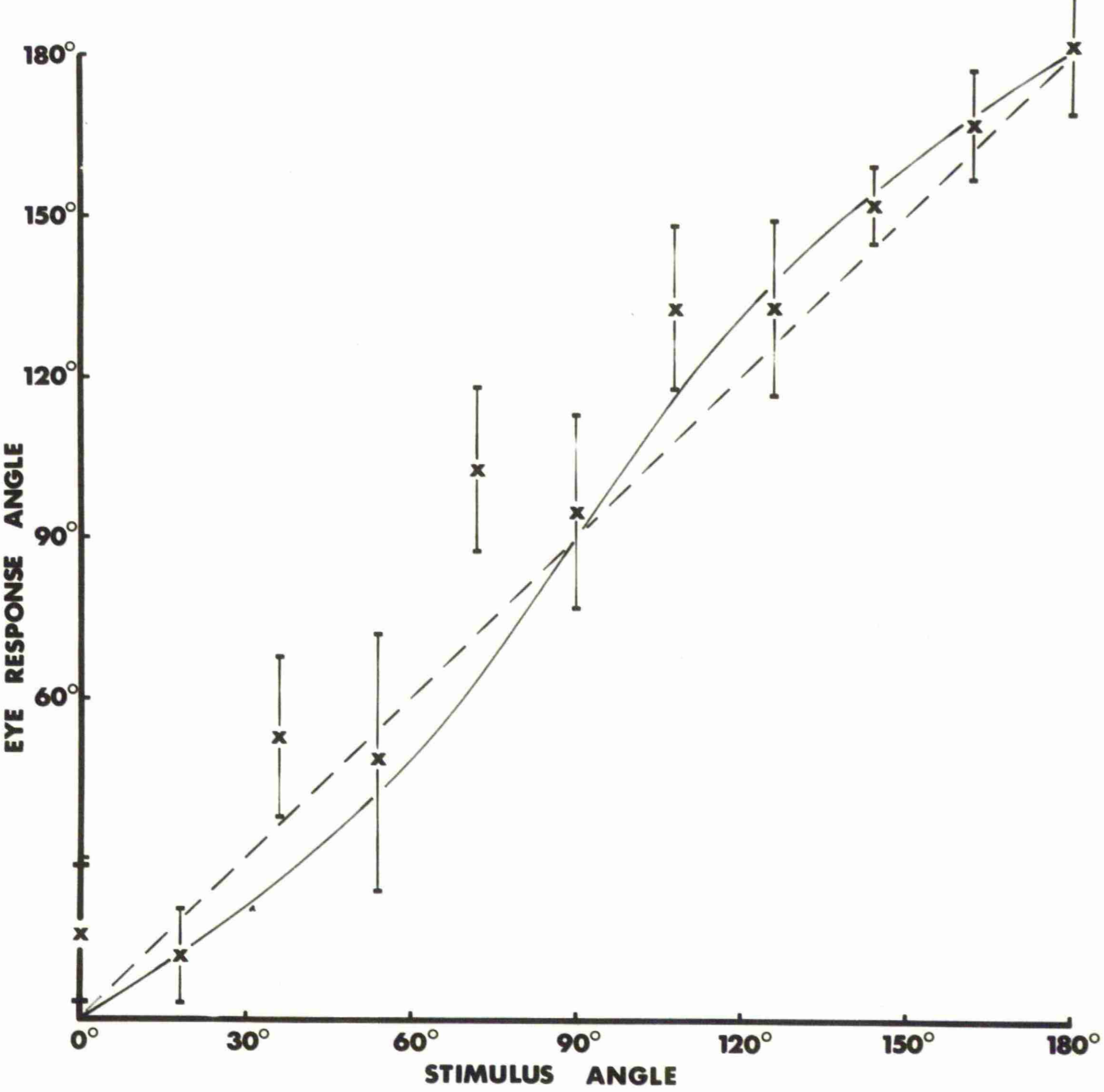

180°
150°
120°
90°
60°
30°
EYE RESPONSE ANGLE
0°
30°
60°
90°
120°
150°
180°
STIMULUS ANGLE
0
·1
·2
·4
·6
·8
1
2·5
2·5
1
·8
·6
·4
·2
·1
0

FIGURE 17.

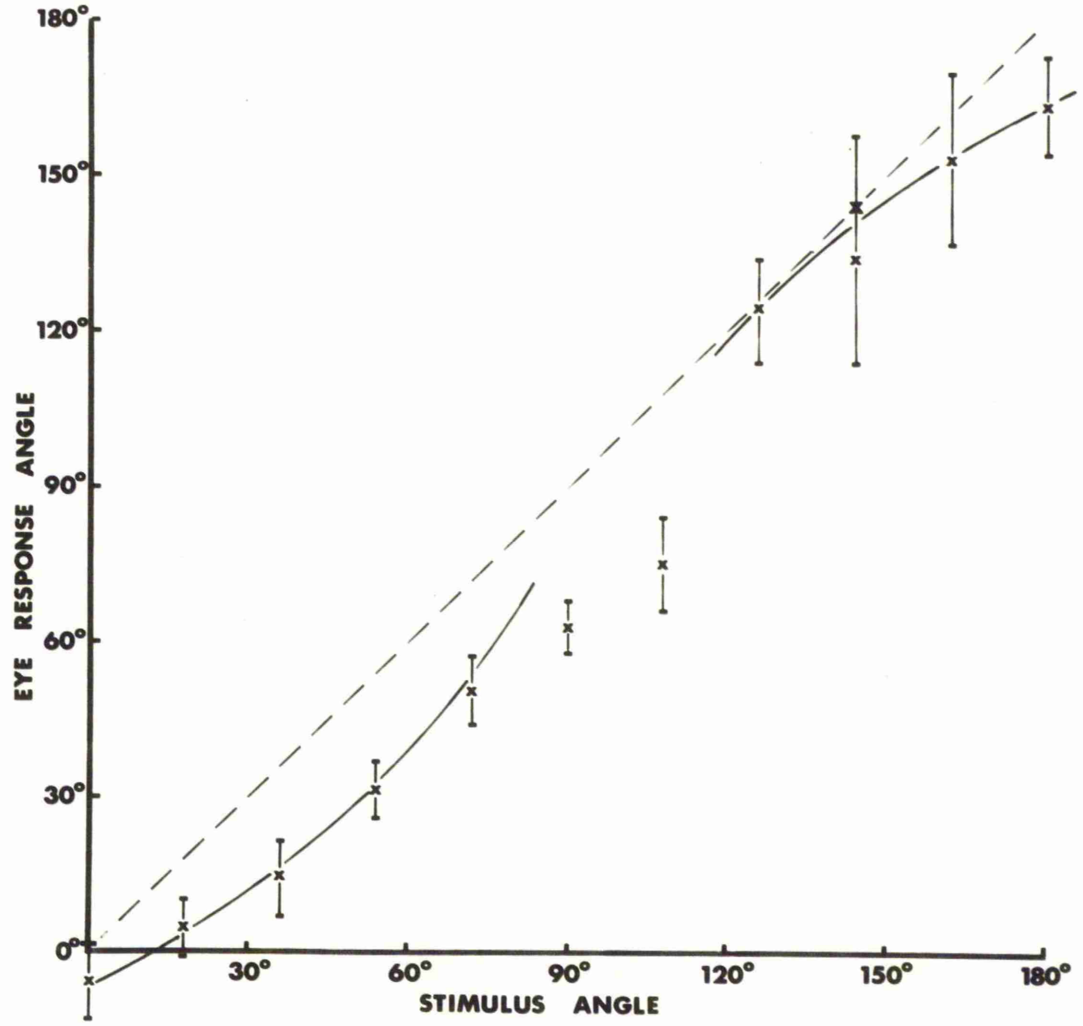
Actual values for the angles of eye movement in response to 5° ramp movements of a pinlight in front of crab at different angles to the horizontal. Stimulus velocity 1°/sec. Vertical lines represent standard deviations from the mean of between 4 and 14 responses. Dashed line represents response = stimulus (i.e. $\frac{V}{H} = 1$). Continuous curve is theoretical curve best fitting the results; it is $\frac{V}{H} = 0.67$.



180°
150°
120°
90°
60°
EYE RESPONSE ANGLE
0°
30°
60°
90°
120°
150°
180°
STIMULUS ANGLE

FIGURE 18.

As Fig. 17 but a different crab. Here the continuous curves represent $\frac{V}{H} = 0.6$ displaced vertically on the graph to fit the data. The large X on the graph opposite the 144° stimulus is the mean response to that stimulus, if one response, rather different from the others, is arbitrarily excluded from the results. Standard deviations are from means of between 8 and 12 responses.


180°
150°
120°
90°
60°
30°
0°
30°
60°
90°
120°
150°
180°
EYE RESPONSE ANGLE
STIMULUS ANGLE

This gives a vertical:horizontal gain ratio of 0.67, for

$$\frac{V}{H} = \frac{0.2}{0.3} = 0.67$$

The theoretical response curve, V/H = 0.67, was thus added to Fig. 17, and can be seen to approximately fit the data, being close to the mean of 7 of the 11 different angles tested, whereas the dotted line (response = stimulus) does not fit the results as well.

The results shown in Fig. 18 are less clear, but certainly bear no relation to the dotted line - response = stimulus. Most of the points fit parts of the theoretical response curve, V/H = 0.6, but only if the theoretical curve is displaced vertically on the graph. This suggests that this crab resolved movements into horizontal and vertical components, but made a constant error in its calculation of the stimulus angle, i.e. its zero point was not the horizontal, but an angle 10° - 12° from it.

The data from other similar experiments fitted theoretical response curves with V/H ratios between 0.5 and 0.7, with the exception of one experiment where the theoretical curve best fitting the results was V/H = 1.5; i.e. in this crab the vertical gain was greater than the horizontal gain.

Though the results of these experiments approximately fit different theoretical response curves, there was nevertheless considerable variation in the results, demonstrating that crabs can measure the angle of movement of a pinlight with an accuracy of only ± 10° - 15°. The gains of the responses were similarly variable, so that any estimation by the crab of the velocity of the movement of the sun or moon across the sky would be liable to an error of ± 5 - 10%. This leads one to the conclusion that any navigational ability that crabs may have, is probably not developed to a high degree, for although it appears that crabs resolve diagonal movements into their horizontal and vertical components, they cannot do this with the accuracy that would be necessary for accurate computation of, e.g. latitude and longitude, although it would be sufficient for an onshore or seaward migration.

Two light experiments.

The preceding experiments have shown that crabs can move their eyes equally well in both horizontal and vertical planes, but there is no evidence that a twisting or torsional movement of the eye is possible. In order to test whether such a movement could be induced, two pinlights were rotated in a clockwise circle in front of the crab. The two lights were on opposite sides of the same circle, equidistant from the centre of rotation. The responses were recorded in the horizontal and vertical planes as usual and were compared to eye tremor occurring when the crab viewed a single stationary pinlight and to the response given to a single pinlight rotated in a circle. The result of such an experiment is shown in Fig. 19. Though the response given to the movement of a

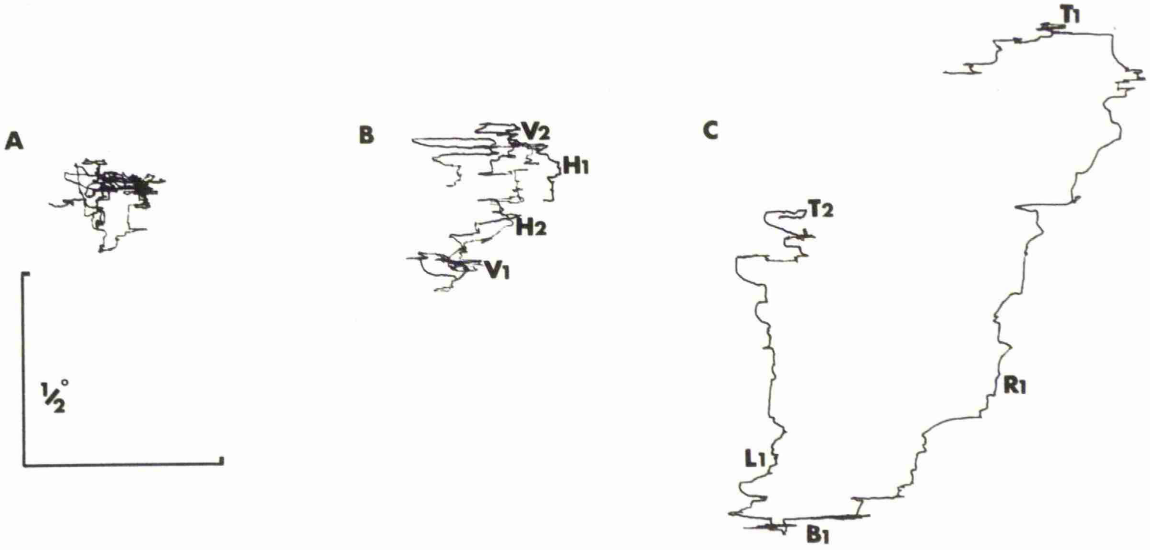
FIGURE 19.

Two-dimensional records of crab eye responses.

A. 40 secs tremor, crab seeing one stationary pinlight.

B. Response to movement of two pinlights in a clockwise circle in front of the crab. The two lights were on opposite sides of the same circle, equidistant from its centre. At H1 the two lights were at 3 o'clock and 9 o'clock, at V1 - 6 o'clock and 12 o'clock, at H2 - 9 o'clock and 3 o'clock, and at V2 - 12 o'clock and 6 o'clock. Stimulus diameter subtended 14.8° at crab's eye. Stimulus frequency - 40 secs/cycle.

C. Response to movement of one pinlight in a clockwise circle in front of the crab. T1, R1, B1, L1 and T2 are the 12 o'clock, 3 o'clock, 6 o'clock, 9 o'clock and 12 o'clock second time around positions of pinlight respectively. Stimulus diameter subtended 14.8° at crab's eye. Stimulus frequency - 40 secs/cycle.


A
B
C
V2
H1
H2
V1
T1
T2
R1
L1
B1
½°

single pinlight was normal and the eye tremor was of the expected amplitude, there were no torsional components in the response to the rotation of the two lights. Instead, the drift and tremor of the eye were enhanced. Though this may be a similar phenomenon to the increase in tremor often associated with an eye response, it may be more simply explained as an increase in motion due to the absence of the stationary pinlight which normally reduced the low frequency components of eye movement.

In all these experiments with pinlight stimuli, the presence of contrasting objects in the visual field inhibited the optokinetic response. However, the presence of a stationary pinlight did not inhibit the response to a second pinlight rotated in a circle around it. A comparison between this response and the response to a single pinlight rotated in a circle of the same diameter showed that the stationary pinlight usually caused a reduction of the response of up to 50% (mean reduction 20%). This suggests that the crab may have been responding to the movement of the centre of light intensity of the two pinlights rather than to the moving pinlight alone.

To test this, two pinlights were rotated in a clockwise circle in front of the crab. The two pinlights were again on opposite sides of the same circle, but were unequal distances from the circle's centre, being distances from it that subtended 8.4° and 2.8° at the crab's eye. A response to the 16.8° diameter circle, but of a lower amplitude than that given to a single light rotated in a circle of that diameter, would suggest that the crab did indeed respond to the movement of the centre of intensity of the two lights. The results of this experiment were, however, equivocal, for the predicted response occurred in only four out of eleven trials, the circles produced by the crab having a mean amplitude 40% less than that given to a single pinlight rotated in a 16.8° diameter circle. In the other seven trials, there was no clearcut response from the crab, though eye drift and tremor were enhanced above normal values.

In the first of these 'two light' experiments, where the lights were on opposite sides of the same circle, equidistant from its centre, the only response of the crab was an increase in eye tremor and drift. Though this is in agreement with the theory that the crab responds to the movement of the centre of the light intensity, it is a negative and thus inconclusive result. The problem is further investigated in the next section.

Apparent movement with stationary lights

As well as responding to the actual movement of a pinlight or pinlights, the eyes of Carcinus have been shown to respond to apparent motion induced by stationary pinlights (Horridge, 1966d).

When a stationary pinlight is switched off and a similar one is turned on nearby, the crab interprets the effect as movement

(Horridge, 1966d), just as we do ourselves. The responses obtained by Horridge fell into two classes, those to stimuli of $1^\circ \pm 0.5^\circ$ to which the crab's responses were comparatively large (5-10% of stimulus), and those to stimuli of 2° or more to which the responses were uniformly small (0.02° - 0.04° in amplitude).

Repetition of this experiment gave results of essentially the same form as those of Horridge. The responses (Fig. 20) usually had a rapid initial phase with a slower follow-up to a plateau. The fast initial phase frequently overshot and was sometimes absent altogether. The response was usually complete within 30 secs. As the experiment was carried out with crabs in the closed loop condition with both eyes free to see and move, the stationary pinlight must have appeared to move across the eye in the reverse direction as a direct consequence of the eye's own movement. Hence it was not surprising that the responses obtained were considerably smaller than those to actual movement of a pinlight through identical angles (compare horizontal responses of Fig. 14 with Fig. 21). The responses graphed in Fig. 21 were all from the same crab though essentially similar results were obtained with five other crabs. In all experiments, the responses increased with increasing stimulus angle and then flattened out to a plateau for stimulus angles above 3° - 4°. At 10°, responses had not decreased significantly. In none of the experiments was there any evidence for the two classes of response obtained by Horridge (1966d).

FIGURE 20.

Record of left eye response to apparent movement of a pinlight in the horizontal plane in front of crab. Closed loop situation with both eyes able to see the stimulus. Movement to the right is shown by a downwards movement of the trace.

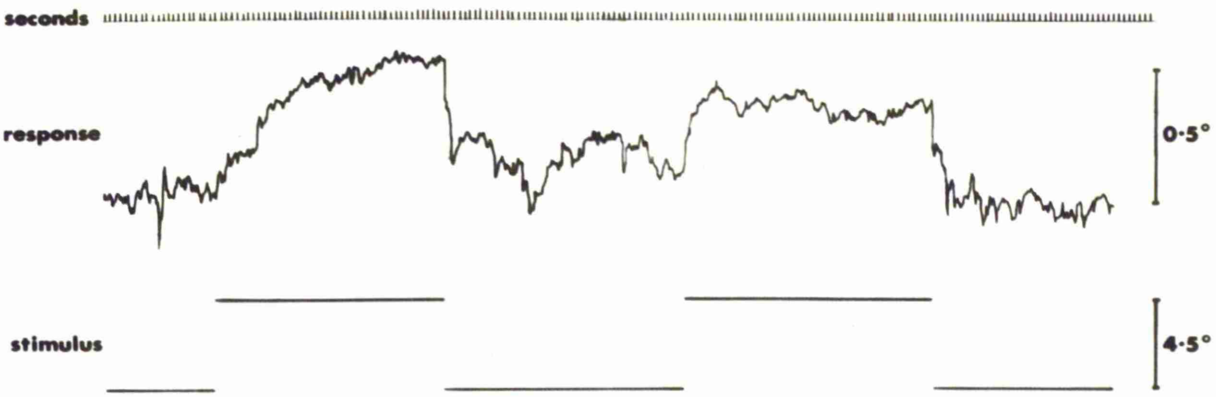
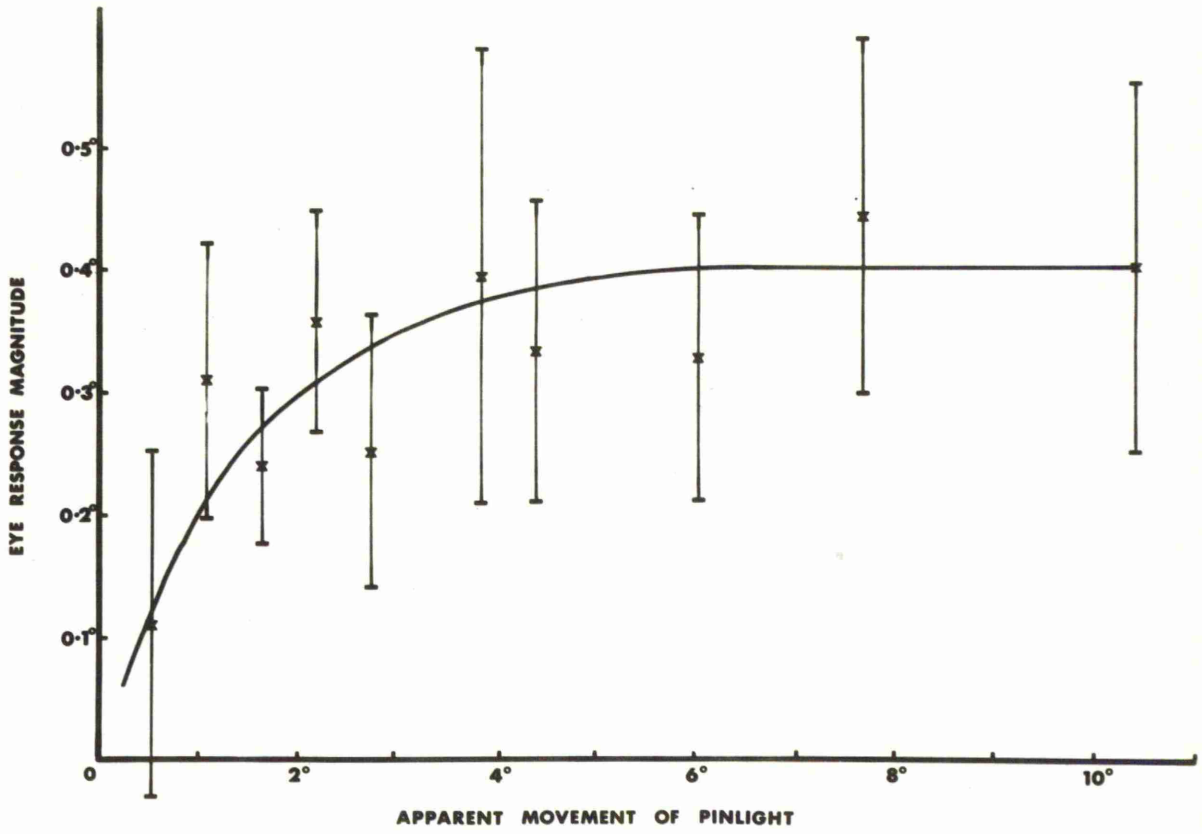

seconds
response
0·5°
stimulus
4·5°

FIGURE 21.

Graph of eye responses to apparent movement of a pinlight in front of crab. Closed loop situation with both eyes able to see the stimulus. Vertical lines represent standard deviations from the mean of between 8 and 25 responses. The curve on the graph was drawn by hand to fit as many experimental points as possible.


EYE RESPONSE MAGNITUDE
0·5°
0·4°
0·3°
0·2°
0·1°
0
2°
4°
6°
8°
10°
APPARENT MOVEMENT OF PINLIGHT

There is thus no reason to believe that responses to apparent movement stimuli of $1^\circ \pm 0.5^\circ$ are the outputs of a movement perception system, while responses to larger stimuli are the outputs of a position sensitive system. The results do, however, give some indication of the angle through which movement correlation occurs. Correlation is good for stimulus angles up to $3^\circ - 4^\circ$ for the crab's responses bear a close relation to the size of the stimulus. However, the responses to stimuli of greater amplitudes bear little relation to stimulus magnitude, suggesting poor correlation. Hence adjacent or subadjacent ommatidia are more likely to be involved in movement correlation than more widely spaced ommatidia. This view supports the detailed analyses of Hassenstein & Reichardt on the beetle <u>Chlorophanus</u> (Hassenstein & Reichardt, 1956; Hassenstein, 1958a, b; Reichardt, 1957, 1961, 1962), McCann & MacGinitie (1965) on the fly <u>Musca</u>, and Thorson (1966a, b) on the locust <u>Schistocerca</u>. An experiment involving optokinetic memory giving essentially the same result as this is described in Section 4 of the "Results".

When an additional light or lights accompanied the first, the mean response was usually increased, though these increases were of low statistical significance due to the large variations between individual responses. In these experiments, eight equally spaced pinlights, the distance between them subtending 0.55° at the crab's eye, were numbered from left to right 1 to 8. A shift from lights 1 and 3 on to lights 2 and 4 on -

from 1 x 3 x x x x x
to x 2 x 4 x x x x

- or from lights 1 and 5 on to lights 2 and 6 on -

from 1 x x x 5 x x x
to x 2 x x x 6 x x

- thus produced a mean response of 20% of the stimulus, while the shift from 1 on to 2 on -

from 1 x x x x x x x
to x 2 x x x x x x

- produced a mean response of 17% of the stimulus, although in all three situations the angle through which the apparent movement occurred was 0.55°. This increase in response was more significant when the number of lights was further increased, for a shift from 1, 2, 3 and 4 on to 2, 3, 4 and 5 on -

from 1 2 3 4 x x x x
to x 2 3 4 5 x x x

- gave a mean response of 30% of the stimulus. Whether this increase was due to spatial summation of the larger number of receptors stimulated, or simply due to the increase in light intensity is not known.

Now in these experiments, there are three different changes to which the crab could have responded. First, the acuity of the eye could be such that the crab saw the lights as separate entities and might therefore have made the same movement correlations as man would. Second, the crab, whether or not it saw the lights as separate entities, might have been responding to edge shifts; i.e. the shift from 1 to 2 and from 4 to 5 (see above). Third, the crab, if it could not distinguish the lights as separate entities, might have responded purely to the shift of the centre of intensity of the lights - i.e. to the shift from a centre of intensity of 2.5 to 3.5 (see above).

To test these three possibilities, different combinations of pinlights were set up. The first was a switch from lights 1, 3 and 8 on to lights 2 and 4 on.

from 1 x 3 x x x x 8
to x 2 x 4 x x x x

Man interprets this as a shift to the right, seeing the shifts 1 to 2 and 3 to 4 as movement. However, the crab's responses were consistently to the left. This could be interpreted as a response to an edge shift (shift from 8 to 4 is greater than that from 1 to 2), or, more likely, a response to the shift in the centre of light intensity to the left.

In the second experiment, the change was from lights 1 and 8 on to lights 1, 2 and 8 on.

from 1 x x x x x x 8
to   1 2 x x x x x 8

Here there is no edge shift, but the crab responded consistently to the left, i.e. in the direction of the shift of the centre of light intensity. It thus appears that the crab does not see closely spaced pinlights, subtending a small angle at the eye, as separate entities, and follows changes in the centre of light intensity rather than edge shifts. This conclusion is in agreement with that of the two light experiments described in the last section, and is a comparable result to that obtained by Horridge & Shepheard (1966) who, using two concentric black and white striped drums as a stimulus, obtained a response against the movement of an edge, but in the direction of the change of the centre of brightness of the drum.

Responses to interacting movements of lights and stripes

Bearing in mind the previous section, preliminary experiments were carried out to see if the responses to the movement of the centre of brightness of an illuminated patch and those to movement of a striped drum interacted in any way.

Initially, the response of the eye to oscillation of a drum of stripe repeat distance 8½° was recorded. Then, with the drum stationary, a bright spot of light, subtending an angle of 32° at the crab's eyes, was played on the drum and oscillated at the same frequency and amplitude. The responses obtained to the movement of the spot were of the order of 20% of the stimulus, while those to the movement of the drum were about 70% of the stimulus. When both the drum and spot of light were oscillated together, 180° out of phase with each other, all the crab's responses were in phase with the drum oscillation, the responses not being significantly smaller than those to the movement of the stripes alone. Even when the drum and spot of light were oscillated in phase, the responses were not significantly larger than those to drum movement along.

Thus the responses to moving stripes completely overwhelm those to a moving light. This is hardly a surprising result, however, when it is considered that the responses to moving stripes are the result of summation from all areas of both eyes, while those to a moving spot of light are necessarily the result of much less widespread interaction.

4) OPTOKINETIC MEMORY

The eyes of crabs have been shown to respond to drum velocities below 0.01°/sec (Horridge & Sandeman, 1964). As the eyes also exhibit continual tremor of 0.01° - 0.2° peak to peak and frequency 1-3 c.p.s., low velocity stimuli must be averaged over several seconds before movement is deduced. Thus, either a memory of past visual input or an integrating system of long time constant, form a necessary part of the response mechanism to these low velocity stimuli.

Optokinetic memory has, indeed, been shown to exist in <u>Carcinus</u> (Horridge & Shepheard, 1966; Horridge, 1966a,b) and in <u>Locusta</u> (Horridge, 1966c). To elicit a memory response, a crab is placed in a stationary striped drum; the drum illumination is then turned out, leaving the crab in complete darkness. The drum is then moved through a small angle in the dark. There is no response from the crab, showing that the drum movement is not seen by the crab. After a few seconds (or even a few minutes), the light is turned on again and the eyes are found to move in the same direction as the drum was moved. For such a reaction to have taken place, it is necessary for the crab to have correlated the present with the previous position of the drum, i.e. it is necessary for the crab to have some memory of the previous position of the drum which it compares with the drum's present position, the mismatch between the two causing the memory response.

The memory response under open and closed loop conditions is illustrated diagrammatically in Fig. 22. In the closed loop situation the response, as it occurs, cuts down the stimulus (i.e. the mismatch is progressively reduced), and the response is 50-80% of the stimulus angle. Under open loop conditions, the seeing eye cannot move, and the response of the blinded eye does not affect the stimulus. The mismatch is thus never reduced, and the response angle thus greatly exceeds the stimulus angle.

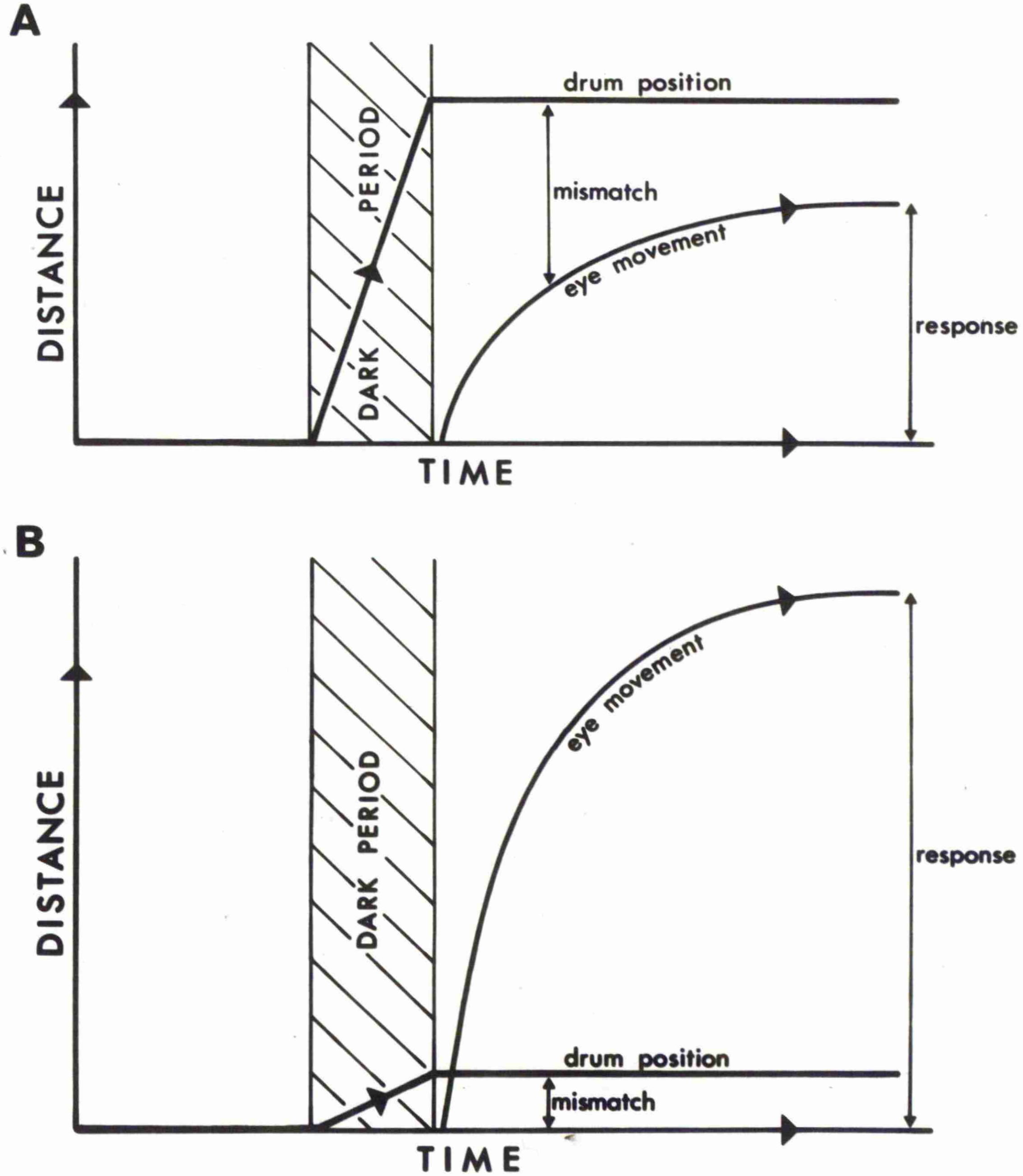
In the following experiments, the time course of the build-up of optokinetic memory is examined, as is the degeneration with time of memory built up to different extents. A model for the memory system is also proposed incorporating both position and velocity negative feedback loops. A comparison of open and closed loop memory responses from the same crab, and measurement of open loop memory responses to a drum of stripe repeat distance 180°, confirms the view that the memory system incorporates both position and velocity components, for these responses cannot be explained in terms of either a pure velocity or a pure position system.

Build-up of optokinetic memory

In order to examine the build-up of memory, the angle through which the drum was moved and the dark period were kept constant; the factor varied was the time during which the crab viewed the drum before it was moved. However, the experiment was not quite as straightforward as this, because crabs' eyes continually exhibit tremor, drift and

FIGURE 22.

Diagrams representing memory responses under closed loop (A) and open loop (B) conditions. The drum is moved during a period of darkness. Upon re-illumination the eye responds by moving in the direction of the drum movement, the input to the eye movement control system being the mismatch between the drum and eye positions. In the closed loop situation, the mismatch is progressively reduced as a direct consequence of the eye's own movement (angle feedback) and the response is 50 - 80% of the stimulus angle. In the open loop, through brain condition, the seeing eye cannot move, so the mismatch is never reduced. The response angle thus greatly exceeds the stimulus angle.


A
DISTANCE
DARK PERIOD
drum position
mismatch
eye movement
response
TIME
B
DISTANCE
DARK PERIOD
eye movement
response
drum position
mismatch
TIME

saccades. Under closed loop conditions, therefore, it would be impossible to measure how long any particular stripe was stimulating any particular part of the retina. Therefore, the eye that viewed the drum was fixed to the carapace, the other eye being covered so that it could not see, but was left free to move.

Under these conditions, the free, blinded eye responded to the movement seen by the fixed eye, the crab being in the open loop condition.

The drum was presented for a predetermined time at a test position (T) and moved during a fixed dark period through an angle of $1/2^{\circ}$ to a response position (R). Since a crab can remember a visual input for more than ten minutes (Horridge & Shepheard, 1966), one visual presentation might well have had an effect on succeeding presentations. For this reason, the visual events were presented in a strictly ordered fashion, as shown in tabular form below.

Light	Drum	Time (secs)
on	R	60
off	R → T	10
on	T	x (test time)
off	T → R	10
on	R	60

First the cycle of events was repeated several times without a test stimulus. There was no response from the crab. The test time was then increased for each successive cycle in a regular manner until the response reached a maximum. Finally, the test time was decreased through the same sequence. In this way the complete history of stimulus presentation was known. Examples of the responses obtained are shown in Fig. 23; here an increase in the test time from 5 to 20 seconds resulted in an increase in the response from 1.3° to 2.4° (i.e. $\frac{\text{response}}{\text{stimulus}}$ = gain increased from 1.7 to 3.2).

When the gain of the eye response was plotted against the test time (Fig. 24), it was observed that the gain of the memory response increased approximately linearly with increasing test time, reaching a plateau of a gain of 10 for test times above 40 seconds. The results of increasing and decreasing series of test times were similar and so were not distinguished from each other on the graph. Memory of one visual input would therefore seem not to have any appreciable effect on a succeeding presentation. The graph shows the results from one crab, though essentially similar results were obtained from many others. It thus appears that memory builds up more or less linearly over a period of 40 to 100 seconds to a plateau representing a gain of between 6 and 30.

There remains, however, the possibility that Fig. 24, instead of representing the build-up of memory, represented the decreasing effect of dark adaptation on the memory response. The above experiment was, therefore, repeated but, instead of the light being turned out, a plain

FIGURE 21.

Recordings of eye responses during an experiment on the build-up of optokinetic memory. Time - upper trace; eye response - middle trace; drum position - lower trace.

The drum, initially in the response position, was moved during a 10 sec period of darkness to the test position for a variable test time. Then, during a second 10 sec dark period, the drum was returned to the response position. Upon re-illumination, the eye response occurred. Eye responses occurring during the test time were ignored. The time trace was interrupted during the periods of darkness.

A. test time 5 secs. B. test time 20 secs.

Movement to the right is shown by a downwards movement of the trace.

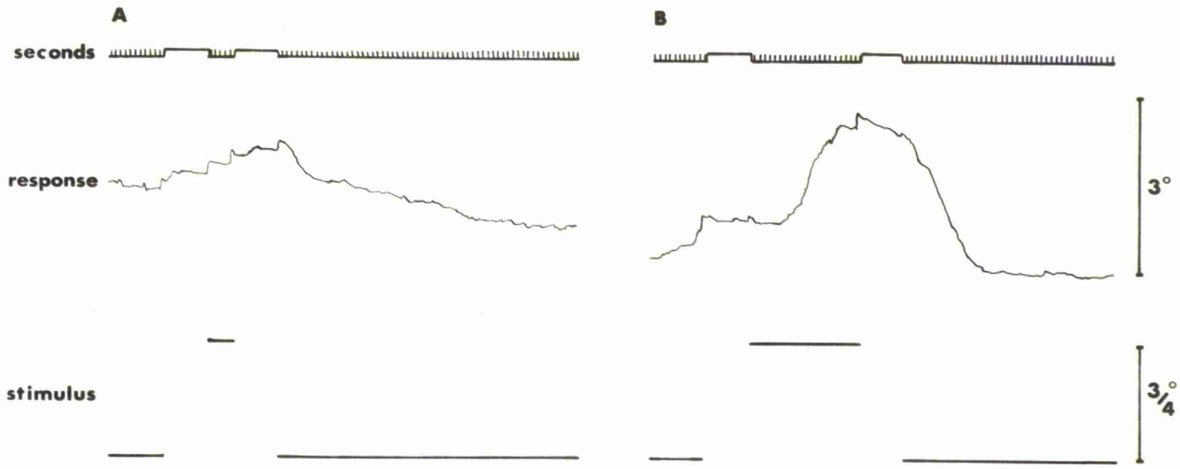
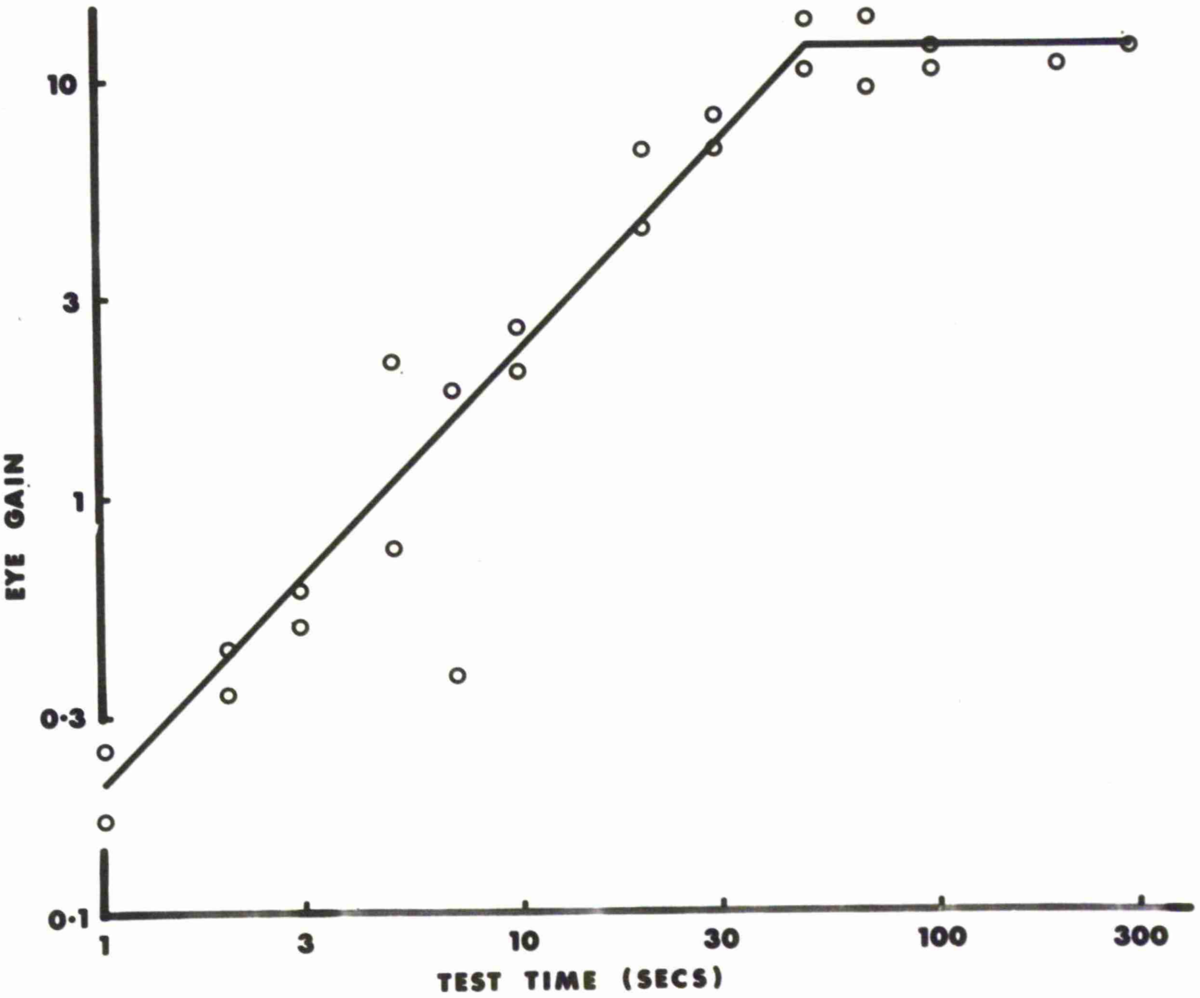

A
B
seconds
response
3°
stimulus
3/4°

FIGURE 24.

The build-up of optokinetic memory under open loop conditions. Drum moved through $\frac{1}{2}^{\circ}$ during periods of darkness. Scale is log : log. Circles are individual responses of the crab. Lines were drawn by hand to fit as many experimental points as possible.


EYE GAIN
10
3
1
0·3
0·1
1
3
10
30
100
300
TEST TIME (SECS)

white cylinder was interposed between the crab and the striped drum. The striped drum was thus moved during the period of time that the crab viewed the plain white background, the movement of the drum being, as before, unseen by the crab. This system obviates the need to turn out the light and thus affect the state of dark adaptation of the crab. The time sequence of stimulus presentation remained exactly the same as before.

The results obtained from several crabs tested in this manner were all essentially similar to those obtained above, a graph of one experiment being shown in Fig. 25. It thus appears that Figs. 24 and 25 do indeed represent the time course of the build-up of optokinetic memory with time.

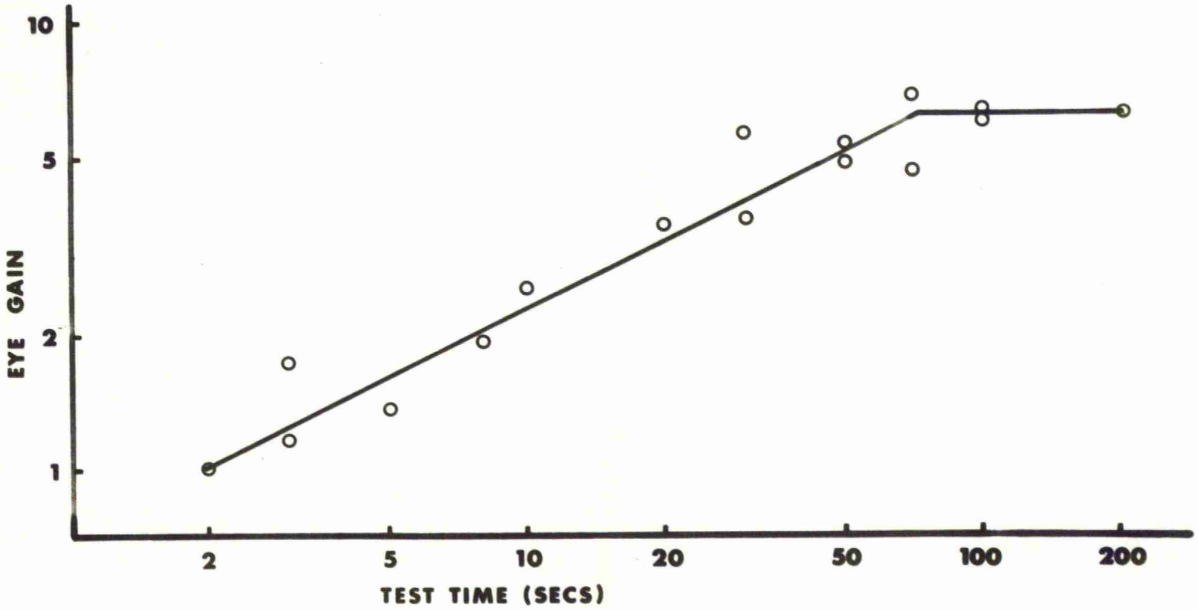
Retention of optokinetic memory

Following the above experiments on the build-up of memory, the degeneration of memory that had been allowed to build up to different extents was examined. It was thought that there might be two different systems, short and long term memory, as are found in mammals.

In order to examine whether this was so, the drum was presented at a test position for a fixed time to a crab in the open loop condition. The factor varied was the length of the dark period during which the drum was moved through an angle of $1/2^{\circ}$ from the test position (T) to the

FIGURE 25.

The build-up of optokinetic memory under open loop conditions. Drum moved through ¾° during periods when a plain white card surrounded the crab. Otherwise as Fig. 24.


10
5
2
1
EYE GAIN
2
5
10
20
50
100
200
TEST TIME (SECS)

response position (R). As in the previous experiment, the visual events were presented in a strictly ordered sequence as shown below.

Light	Drum	Time (sec)
On	R	60
Off	R→T	10
On	T	x (fixed test time)
Off	T→R	y (dark period)
On	R	60

In different experiments, test times of 10, 50 and 70 seconds were chosen. The only variable within an experiment was the length of the dark period (y). The cycle of events was first carried out with a dark period of 10 seconds, and repeated until consistent responses were obtained. The dark period was then increased for each successive cycle until the response was considerably reduced.

Examples of the responses obtained are shown in Fig. 26; here an increase in the dark period from 10 to 30 secs resulted in a decrease in the response from 4.8° to 3.5° (i.e. gain decreased from 9.6 to 7.0). When the gain of the eye response was plotted against the length of the dark period for each of the three test times used (Fig. 27), it was observed that the gain of memory built up for a short time (i.e. test time of 10 secs) degenerated with time, as did memory built up for longer times (i.e. test times of 50 and 70 secs). Although memory built up for 10 secs degenerated to a low value in a shorter time than memory

FIGURE 26.

Recordings of eye responses under open loop conditions during an experiment on the degeneration of optokinetic memory. Time - upper trace; eye response - middle trace; drum position - lower trace.

The drum, initially in the response position, was moved during a 10 sec dark period to the test position for a fixed time. Then, during a second variable dark period, the drum was returned to the response position. Upon re-illumination, the eye response occurred. Eye responses occurring during the test time were ignored. The time trace was interrupted during the periods of darkness.

A. test time 50 secs; dark period 10 secs.

B. test time 50 secs; dark period 30 secs.

Movement to the right is shown by a downwards movement of the trace.

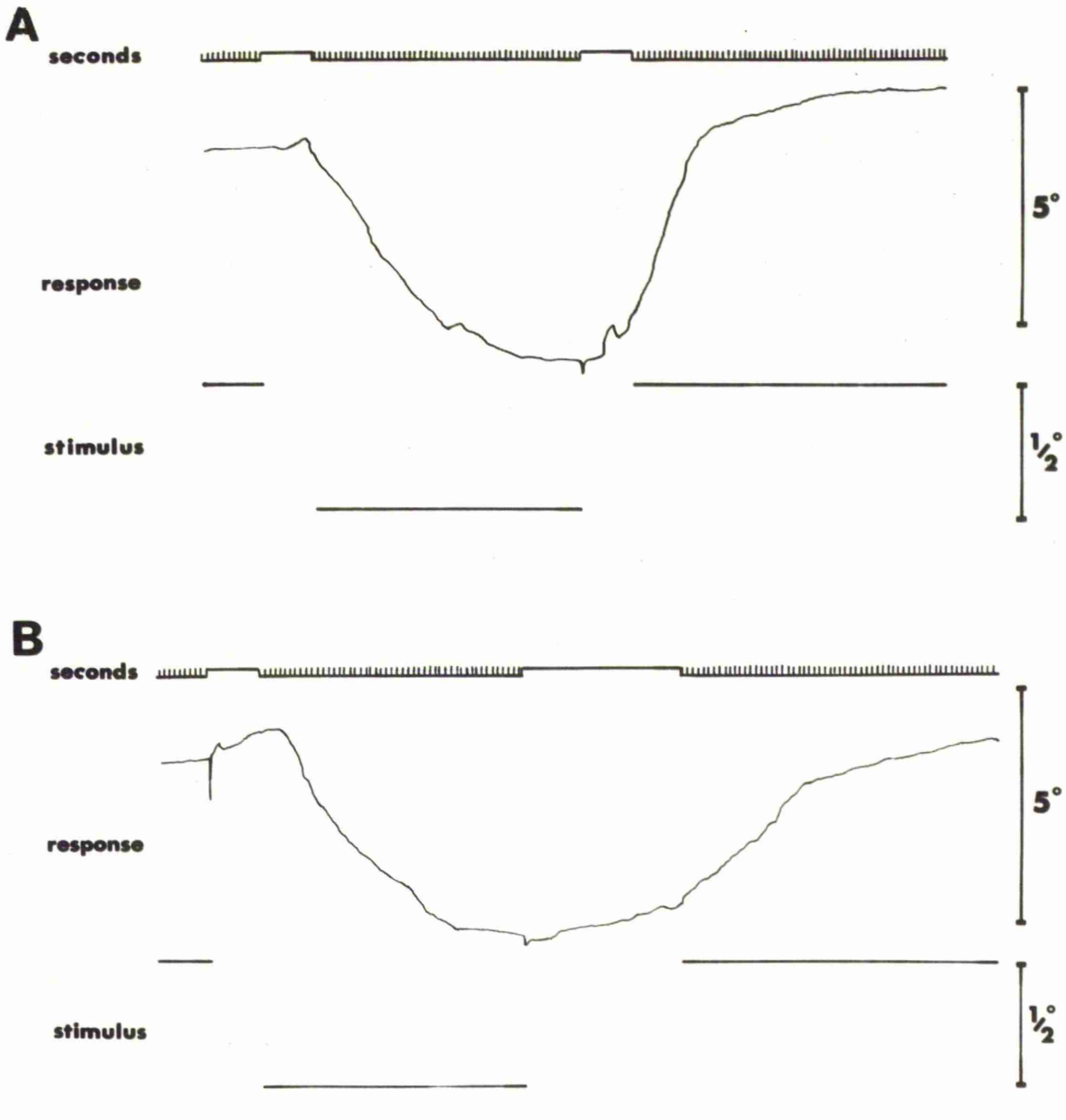
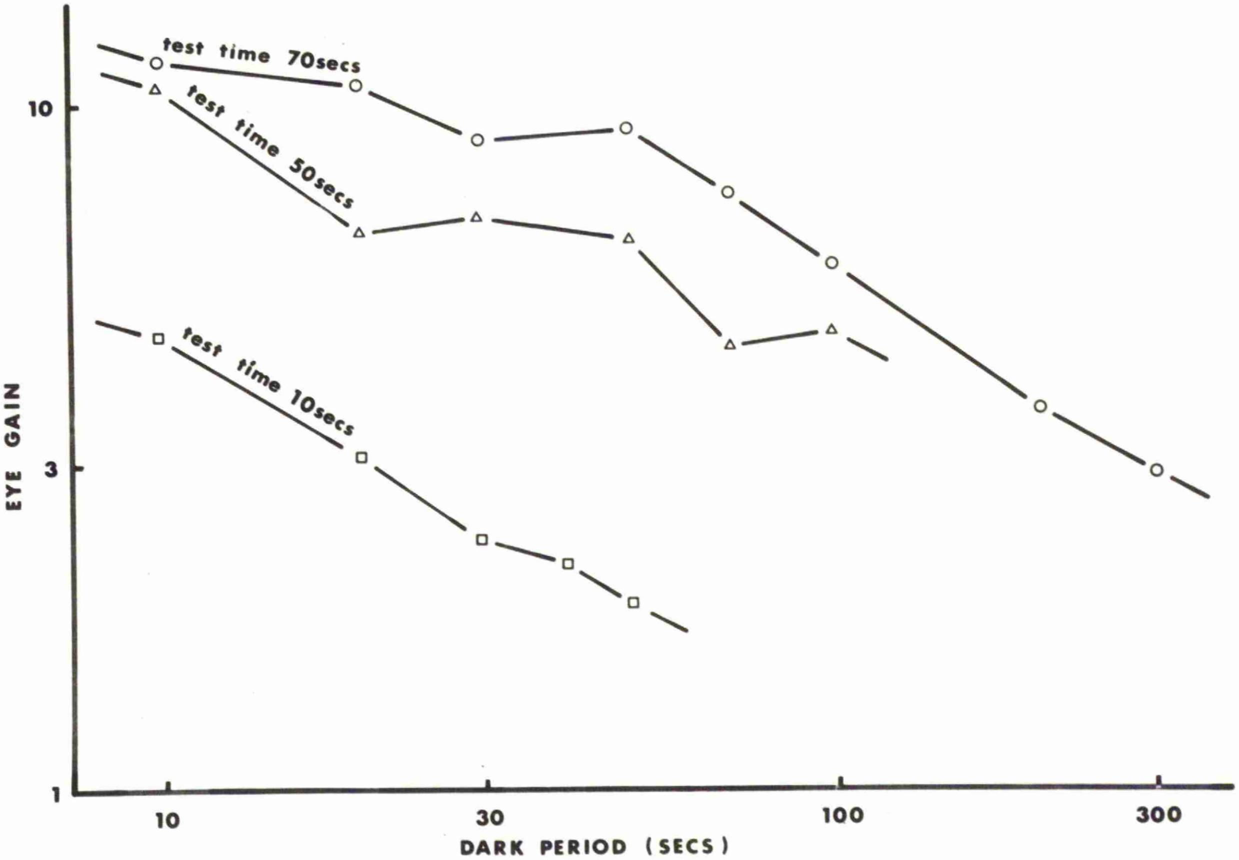

A
seconds
response
5°
stimulus
1/2°
B
seconds
response
5°
stimulus
1/2°

FIGURE 27.

The degeneration of optokinetic memory built-up to different extents under open loop conditions. Drum moved through $\frac{1}{2}^{\circ}$ during periods of darkness. Scale is log : log. The points on the graphs represent individual responses of the crab.



test time 70secs
test time 50secs
test time 10secs
EYE GAIN
10
3
1
10
30
100
300
DARK PERIOD (SECS)

built up for the longer periods, the initial gain of memory built up for 10 secs was considerably lower than those of memory built up for either 50 or 70 secs. There is thus no reason to infer different physiological processes for the retention of memory allowed to build up for different periods of time.

The graph obtained for the degeneration of memory allowed to build up for 70 secs is essentially similar to that obtained under closed loop conditions by Horridge & Shepheard (1966). Breaking the visual feedback loop seems, therefore, not to affect the retention of memory.

The optokinetic memory control system

The above experiments indicate that optokinetic memory takes 40-100 secs to build up and may be retained for several minutes; yet they give little insight into the mechanism by which a crab executes a memory response. In this section, a model is described and tested which, though undoubtedly an over-simplification of the existing system, nevertheless indicates the general mechanisms involved in memory responses.

In a closed loop memory response, the stimulus (the mismatch between the present position and the remembered position of the stripes) is progressively reduced as a direct consequence of the eye's own movement. However, in the open loop situation, the eye that moves is blind, so there is no reduction of the stimulus, which remains the same no matter how far the eye moves. There is thus a negative feedback loop in the memory control system which, in the normal (closed loop) situation, reduces the stimulus angle and is therefore a position feedback loop.

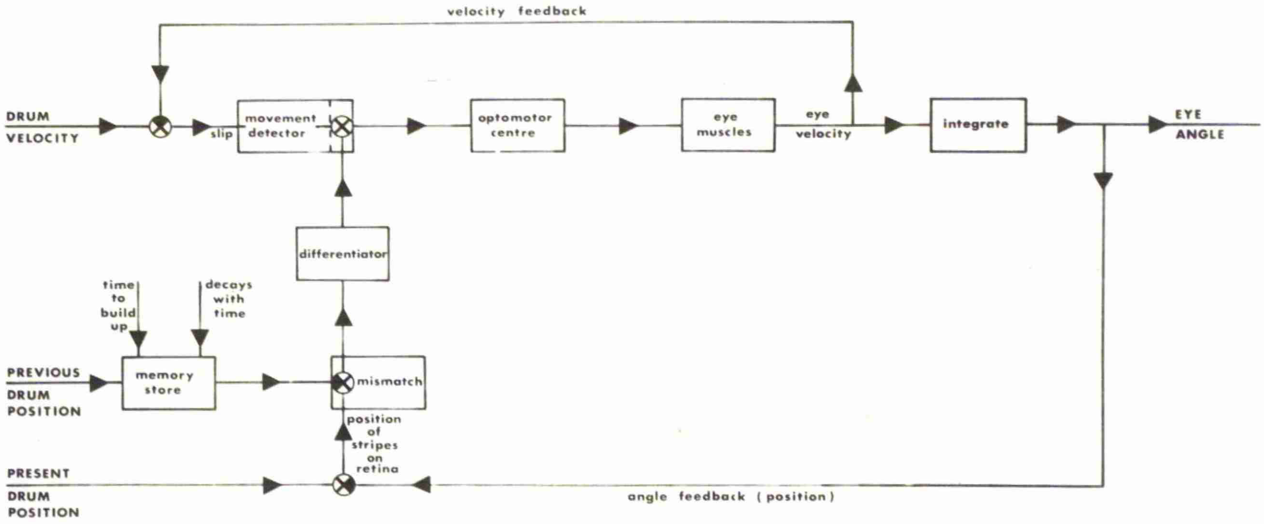
This is not the only feedback loop involved however, for, during the course of a closed loop memory response, the drum must appear to move across the eye in the opposite direction to the eye's own movement. This is because the eye moves across a stationary drum.

In the open loop situation, the moving eye is blind, so no apparent movement is seen. This is evidence for a second feedback loop in the control system which, in the closed loop situation, gives the eye the appearance of movement occurring in the opposite direction to the eye's own movement. It is thus best described as a negative velocity feedback loop. Though both of these feedback loops are integral parts of the memory control system illustrated in Fig. 28, they are external to the animal and are therefore not parts of the memory mechanism.

As shown in Fig. 28, the input to the crab in the memory situation is the position of the stripes on the retina. This position must in some way be compared with a spatially remembered version of the previous position of the stripes, the mismatch between the two being the stimulus for the response. Thus to some extent, memory is a position sensitive system. However, memory is neither instantaneous nor absolute (it takes time to build up and decays with time) so the response does not depend entirely on the amplitude of the mismatch,

FIGURE 28.

The control system for optokinetic memory, incorporating inputs for both memory and velocity stimuli. See text for explanation.


velocity feedback
DRUM VELOCITY
slip
movement detector
optomotor centre
eye muscles
eye velocity
integrate
EYE ANGLE
differentiator
time to build up
decays with time
PREVIOUS DRUM POSITION
memory store
mismatch
position of stripes on retina
PRESENT DRUM POSITION
angle feedback (position)

but will vary with the length of the time that the crab saw the stripes in their initial position, and the length of the intervening dark period.

The perception of velocity by the compound eye also involves correlation of change of position with time (Reichardt 1961; Thorson 1966b). Thus the comparison of present and past drum positions in the memory situation may be a similar process, except in the length of its time constant, to that occurring in velocity perception. If this is so, then it is a reasonable prediction that the mismatch signal is differentiated to velocity and fed into the control system for following optokinetic responses. Certainly, the memory and velocity systems must converge at some stage in the animal, since the same eye muscles are used for both responses. That the two eyes of a crab interact with each other similarly for both velocity and memory stimuli, the information channel linking the eyes being on the sensory side of the brain (see Section 6 of the "Results"), suggests that this convergence of the memory and velocity systems occurs in the periphery.

The control system for memory thus incorporates the velocity control system illustrated in Fig. 8B. In the block diagram (Fig. 28), the velocity amplifier is broken down into its three known constituents; a *movement detector* located on the sensory side of the brain, probably in the optic lamina or medulla; a centre, called the *optomotor centre,* of unknown location which converts sensory impulses signalling movement into motor impulses to the eye muscles, and thirdly, the *eye muscles* themselves.

During the course of a closed loop memory response, the stationary drum appears to move across the eye in the reverse direction as a consequence of the velocity feedback loop; yet the memory response is not inhibited in any way. It was thus thought probable that all information from movement detectors was ignored during the course of a memory response. However, the following experiment (Horridge, 1966g) demonstrates that this is not so and that the eye sees normally during a memory response.

The crab faced a stationary striped drum; the light was turned out and the drum was moved through a small angle in the dark. The light was then turned on and the drum was oscillated at a frequency of 0.5 c.p.s. and peak to peak amplitude 0.2°. The eye responded to the small oscillations, which were superimposed on an apparently normal memory response. Therefore, moving stimuli are not ignored, the eye seeing normally during a memory response.

It is thus necessary to add a velocity input (labelled DRUM VELOCITY) to the block diagram (Fig. 28), which now represents the control system for both memory and following optokinetic responses.

In the above description, the control system for memory incorporates both position and velocity components. Memory responses under open and closed loop conditions were thus compared to see if they were compatible with such an intermediate system, or were better explained in terms of either a pure velocity or a pure position system. Fig. 29 shows the

FIGURE 29.

Comparison of memory responses under closed and open loop conditions. Both graphs represent the responses of the same crab.

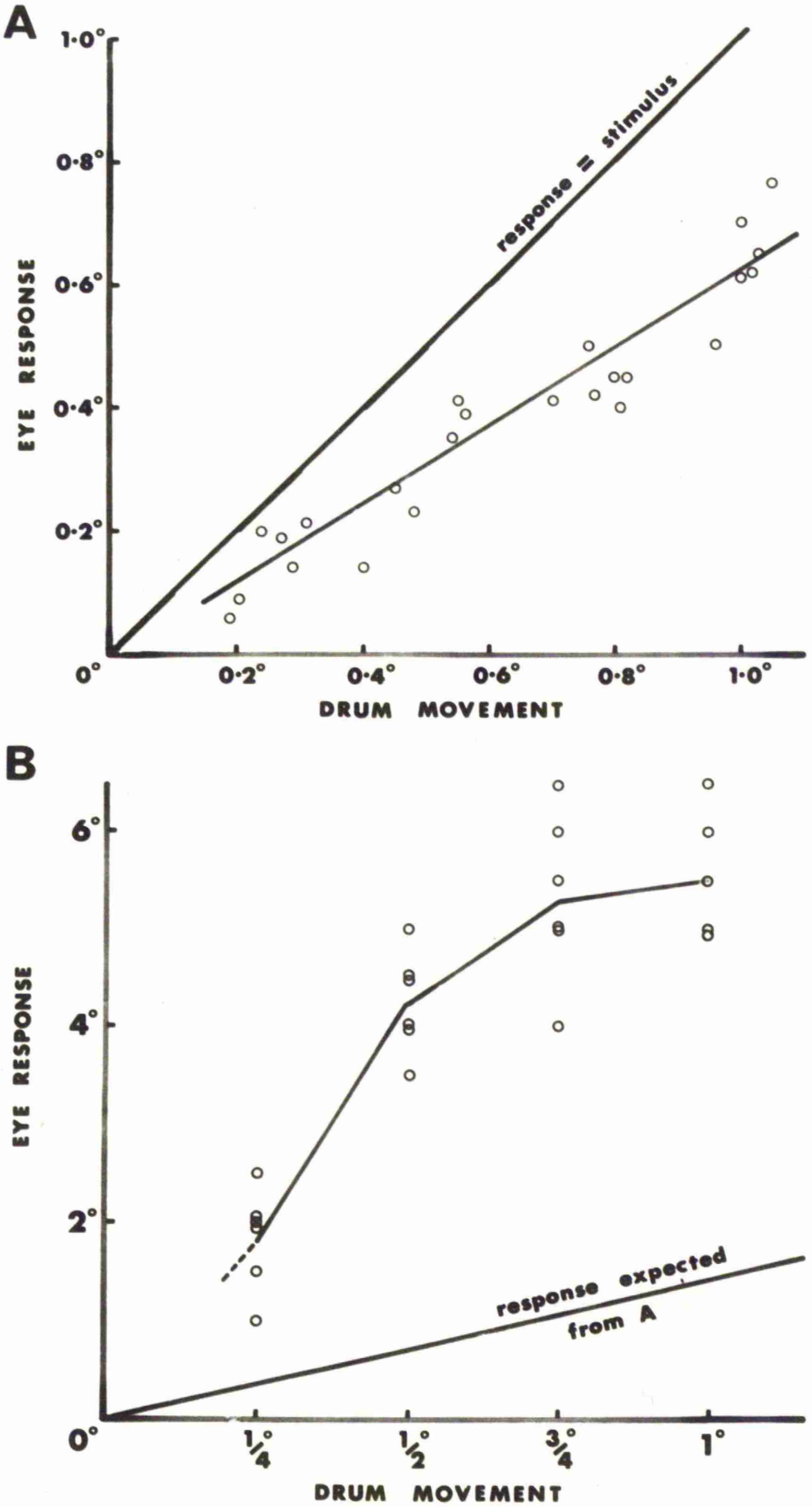
X - axes - angle through which the drum was moved during a dark period of 3 secs.

Y - axes - angle through which eye responded.

A - closed loop responses - line drawn through the points represents a 62% response.

B - open loop responses - straight lines join the means of the responses to the different stimulus angles.

As described in the text, the open loop response was much greater than the theoretical response calculated from the mean closed loop response, on the assumption that memory responses are governed solely by a velocity system.


A
1·0°
0·8°
0·6°
0·4°
0·2°
EYE RESPONSE
0°
0·2°
0·4°
0·6°
0·8°
1·0°
DRUM MOVEMENT
response = stimulus
B
6°
4°
2°
EYE RESPONSE
0°
1/4°
1/2°
3/4°
1°
DRUM MOVEMENT
response expected from A

results of such a comparison of the open and closed loop memory responses of the same crab. If the memory responses could be described solely in terms of the velocity control system as predicted by Horridge (1966a), then the gain (G) of the control system amplifier may be calculated from the mean closed loop response.

$$G = \frac{R}{S-R} = \frac{0.62}{1-0.62} = 1.6$$

(R = response; S = drum angle; mean closed loop response from Fig. 29A is 62 per cent of drum angle).

From this it follows that the open loop responses should have been 1.6 x the drum angle, as shown by the theoretical line on Fig. 29B. However, the open loop responses ranged from 7x the stimulus (for 0.25° stimulus) to 5x the stimulus (for 1° stimulus), far greater than those predicted. A pure velocity system thus does not adequately describe the responses. If a pure position system were involved, the responses of the crabs under open loop conditions should have borne no relation to the stimulus amplitude, for the mismatch is never reduced under open loop conditions no matter how far the eye moves. As the open loop response increased with increasing stimulus angle up to a stimulus angle of 1° at least, a pure position system seems not to fit the data either. However, open loop memory data of Horridge (1966a) could well be described by such a pure position system, even though they were not so described by Horridge.

As a further check on whether or not a pure position system adequately described the memory response, open loop memory responses to a drum of stripe repeat distance 180° (i.e. four black-white edges) were recorded. The result of one such experiment, illustrated in Fig. 30, showed that such a drum had the advantage of reducing the gain of the crab's responses. There was now no doubt that, up to a stimulus angle of at least 2°, the responses increased with increasing stimulus angle, the increase being an approximately linear one in this experiment. A pure position system thus does not describe the responses any better than a pure velocity system, the responses being best described by an intermediate system with both velocity and position components. The system described herein for optokinetic memory, illustrated in Fig. 28, is just such an intermediate system.

The open loop memory responses of Fig. 30 also give an indication of the area over which the eye correlates in the memory situation. Like the apparent movement experiments described in Section 3 of the "Results", the amplitude of the memory responses only bore a close relation to the stimulus amplitude for stimulus angles of up to 2° - 4°. This suggests that accurate correlation can only occur between adjacent and probably subadjacent ommatidia. However, memory responses occurred to stimulus angles of up to at least 80°; thus some degree of integration, perhaps by wide field units, can occur over a much larger area of the eye than this. That memory responses under closed loop conditions

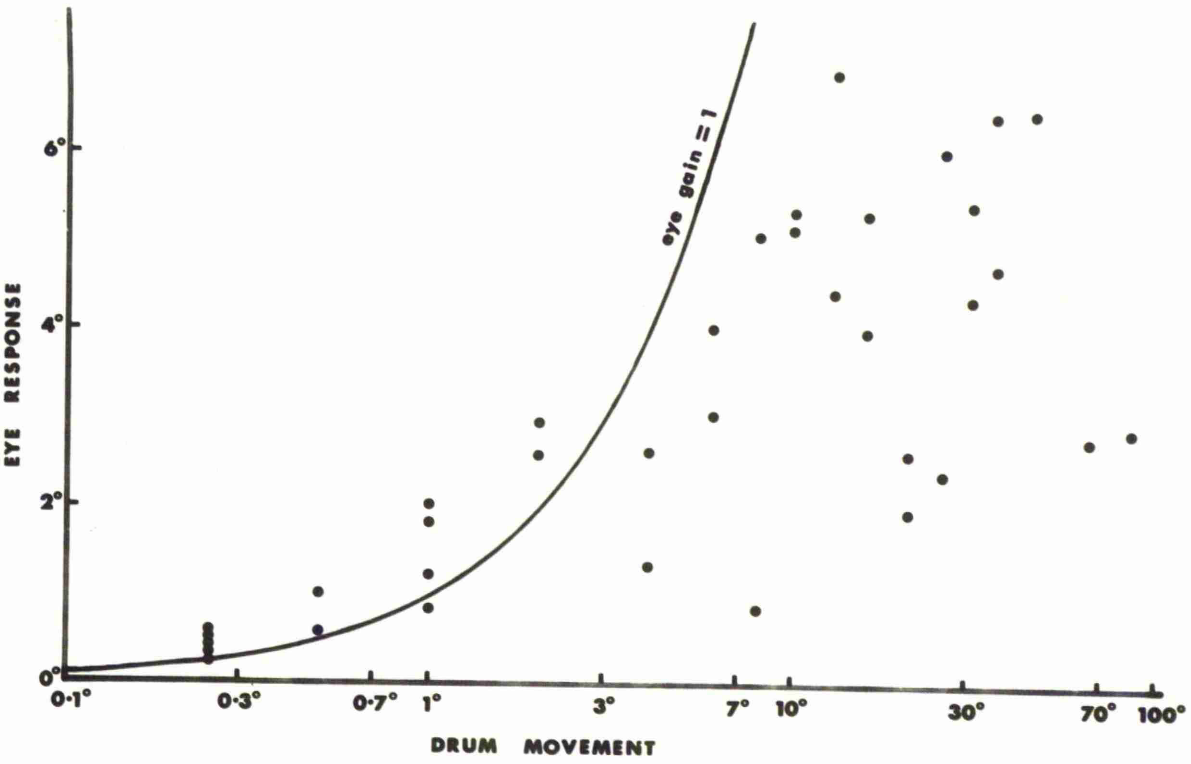
FIGURE 30.

Memory responses under open loop conditions to movement during a dark period of 3 secs of a drum of stripe repeat distance 180°
(i.e. a drum with 2 black and 2 white stripes).

X - axis - log scale:- angle through which drum was moved in the dark.

Y - axis - linear scale:- angle through which eye responded.

Curve is response angle = stimulus angle (i.e. gain of 1).


EYE RESPONSE
0°
2°
4°
6°
eye gain = 1
0·1°
0·3°
0·7°
1°
3°
7°
10°
30°
70°
100°
DRUM MOVEMENT

have been obtained to stimulus angles of over 100° by Horridge & Shepheard (1966) to some extent confirms this conclusion.

5) RESPONSES TO RAMP AND STEP STIMULI

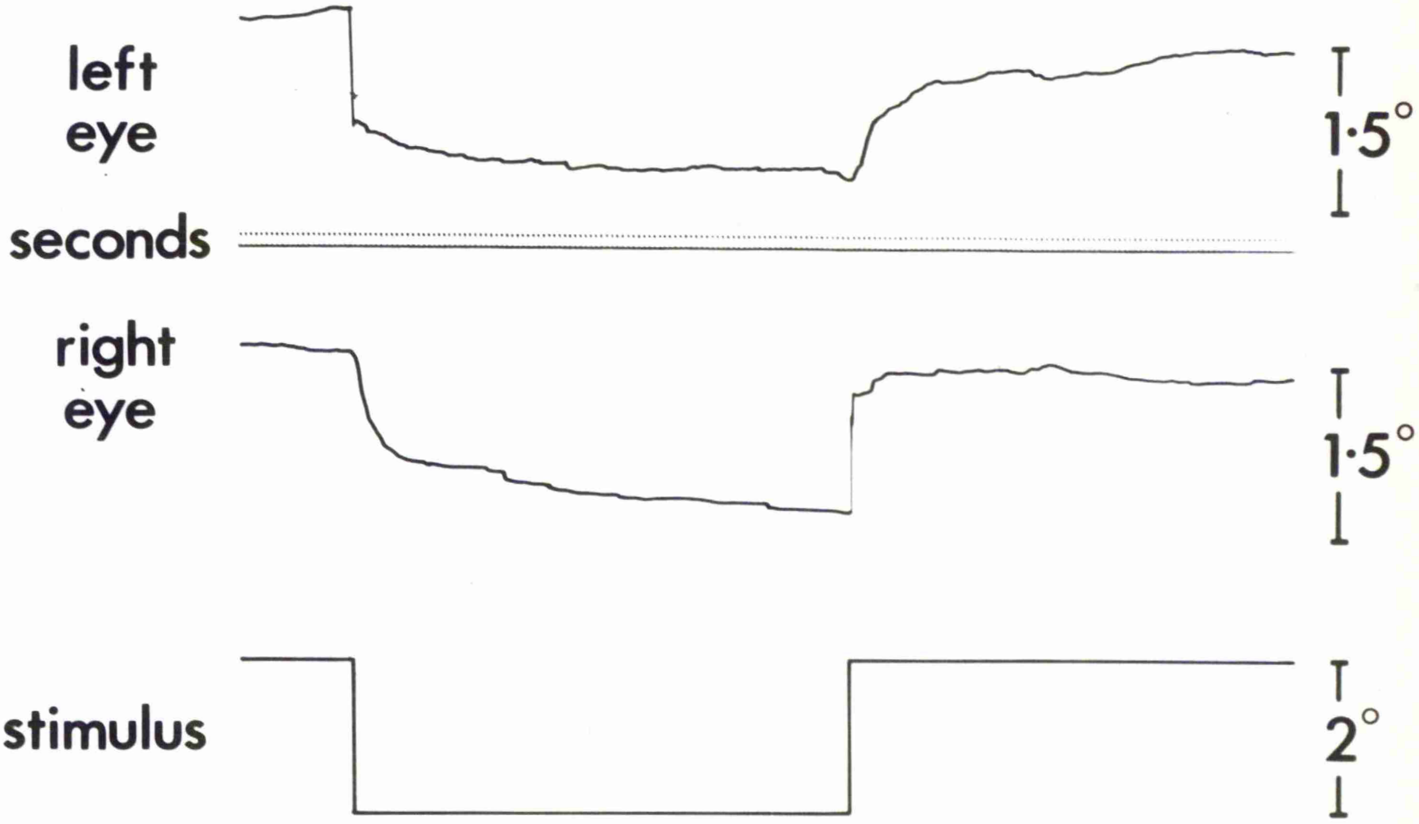
Ramp and step functions are two of the commonest transients used by control system engineers in the analysis of feedback systems. In the Crustacea, these functions have only previously been used by Horridge (1966f) who employed step movements of a striped drum in the analysis of the adaptation of the optokinetic response of Carcinus. In the following experiments, ramp and step movements of a striped drum were used to elicit eye movements in crabs in order to analyse the part played by optokinetic memory in the crab's normal optokinetic response. Theoretically the response to a ramp or step stimulus would have a memory component if the crab, as well as responding to the actual movement of the drum (velocity response), compared the final position of the drum with its initial position, the mismatch between the two causing eye movement.

Step functions

If memory does play any part in normal optokinetic responses, it should be most apparent in the responses to step functions, since, in these stimuli, the duration of the movement of the drum is short. The eye responses to $1/4^{\circ} - 2^{\circ}$ step movements of the striped drum were thus recorded under closed loop conditions. As illustrated in Fig. 31, there were usually two components to the eye response.

FIGURE 31.

Record of responses of both eyes to 2° step movement of a striped drum. Movement to the right is shown by a downwards movement of the trace. Note that there are two components to the eye response, an initial fast movement followed by a slow movement. The initial fast movement was greatest when the eye saw a step movement towards the midline.


left
eye
1·5°
seconds
right
eye
1·5°
stimulus
2°

The first of these, a fast movement, occurred during or immediately after the drum movement. Its amplitude was greater in responses occurring towards the crab's midline than in those occurring in the opposite direction. This component of the response is presumed to be the velocity response to the actual movement of the drum.

The second component of the response was a much slower movement which gradually decreased to zero. It was sometimes complete in ten seconds but frequently lasted for more than a minute. As it occurred after the drum had stopped moving, the stripes must have appeared to move across the eye in the opposite direction to the movement and as a direct consequence of it. Yet the response was not inhibited. All of these properties are characteristic of memory responses.

The open and closed loop responses to step stimuli were thus compared, to test whether they were compatible with a system that included a memory component. As shown in Fig. 32A, the eye movement under closed loop conditions was always less than the drum movement (i.e. response<stimulus), the mean response being 65% of the stimulus. Under open loop conditions, the eye responses were far greater than the step stimuli and ranged from a mean of 13x the stimulus for a $\frac{1}{2}^{\circ}$ step to a mean of 7.5x the stimulus for a 1° step (Fig. 32B).

The simplest hypothesis concerning the responses to step stimuli, namely that they are entirely explicable in terms of the velocity

FIGURE 32.

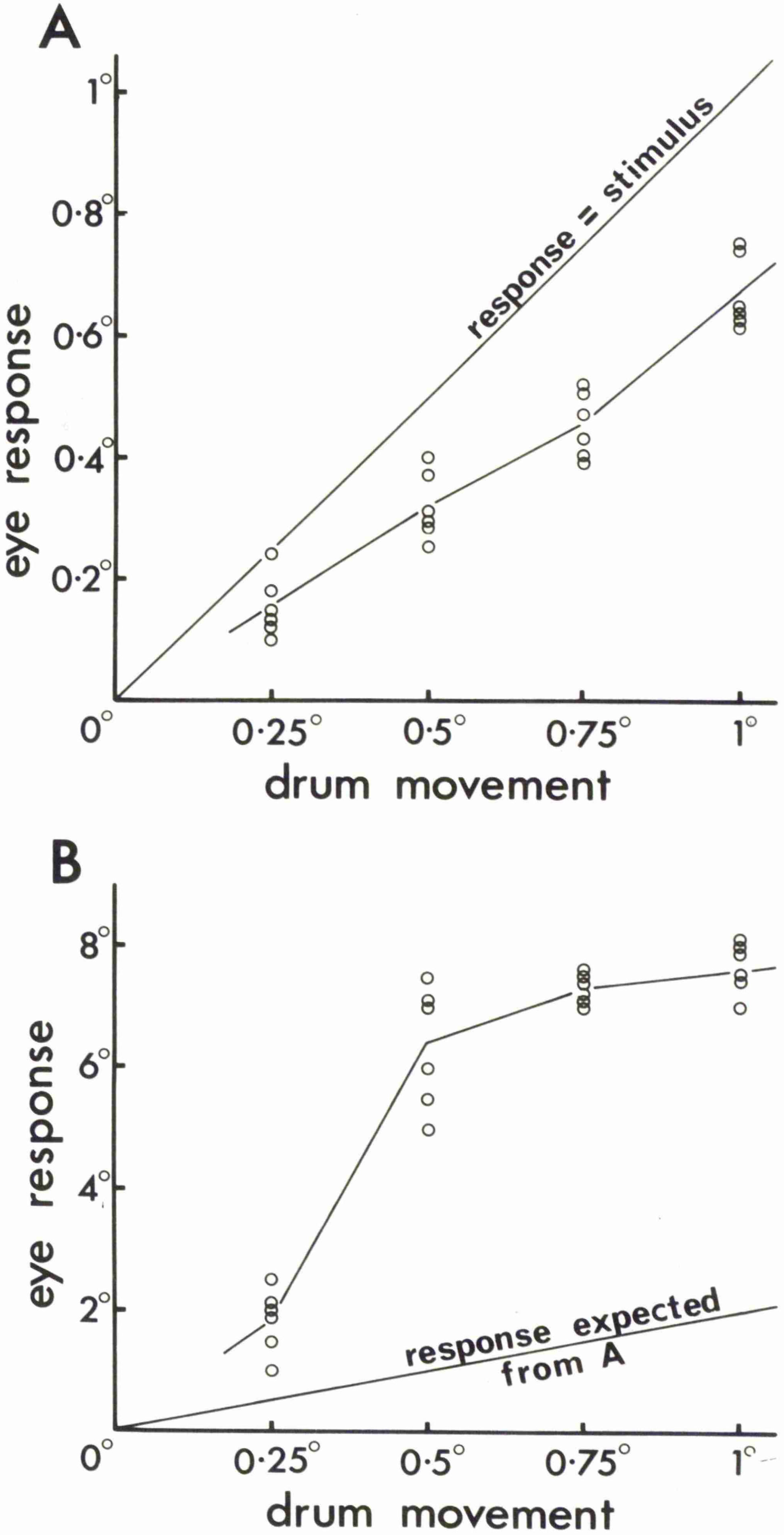
Comparison of responses to step stimuli under (A) closed loop and (B) open loop conditions:-

X - axes - angle through which the drum was moved.

Y - axes - angle through which the eye responded.

Straight lines join the mean of the responses to the different stimulus angles.

As described in the text, the open loop response was much greater than the theoretical response calculated from the mean closed loop response, on the assumption that step responses are governed solely by the velocity system.


A
1°
0·8°
0·6°
0·4°
0·2°
0°
eye response
response = stimulus
0·25°
0·5°
0·75°
1°
drum movement
B
8°
6°
4°
2°
0°
eye response
response expected from A
0·25°
0·5°
0·75°
1°
drum movement

control system, may be simply checked by reference to the results of Fig. 32. If there is no memory component to the responses to step stimuli, the gain (G) of the control system amplifier may be calculated from the mean closed loop response in the following way:-

$$G = \frac{R}{S-R} = \frac{0.65}{1-0.65} = 1.9$$

(R = mean closed loop response.
S = stimulus angle).

Since, under open loop conditions R=G.S, open loop responses of 1.9 x the stimulus would be expected from the above calculation, as shown by the theoretical line on Fig. 32B. However, as stated above, the open loop responses were far greater than this, ranging from 7.5 x the stimulus to 13 x the stimulus. Therefore, the responses to step stimuli cannot be described solely in terms of the velocity control system and there must be a second constituent to the responses.

There are good reasons for believing that this second constituent is memory. First, as described earlier, the second of the two components of the response to a step stimulus has several of the characteristics of a memory response. Second, open loop memory responses are far greater than can be predicted from closed loop memory responses on the assumption that memory may be described solely in terms of the velocity control system (Fig. 29). Since the result obtained above for the comparison of open and closed loop step responses is similar to this, it is reasonable to assume that the second component of the response to a step stimulus is optokinetic memory.

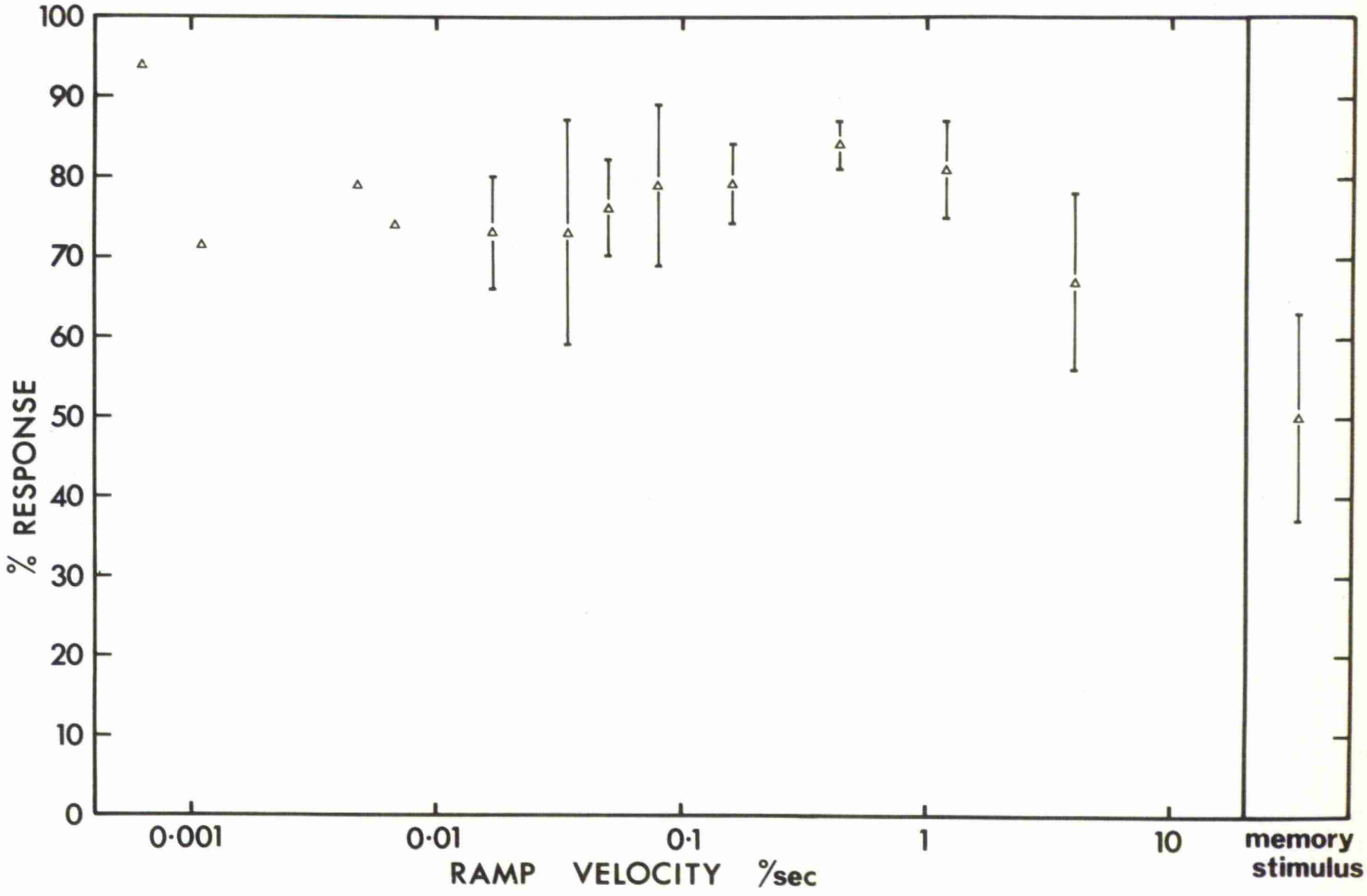
When the responses to step and memory stimuli were compared directly (Figs. 29 and 32), it was observed that open and closed loop step responses had a higher gain and lower variability than, respectively, open and closed loop memory responses. Though the responses of Figs. 29 and 32 were from different crabs, the same result was obtained when all the data came from the same crab (Fig. 33 - 4°/sec ramp stimulus is equivalent to the step stimulus described above). These differences in gain are readily explained when a step stimulus is considered as a memory stimulus with a velocity component, this latter component being necessarily absent from a pure memory stimulus. In the responses to both memory and step stimuli, open loop data showed far greater variability than closed loop data. However, this was not unexpected, for it is a property of negative feedback loops to decrease response variability.

Ramp functions

Eye responses to ramp movements of a striped drum in the velocity range of 0.0006°/sec to 4°/sec were also recorded and compared to memory responses. The graph, Fig. 33, shows the closed loop responses of one crab plotted as a percentage of the stimulus angle. The points on the graph have not been connected, since it is doubtful whether the changes in the mean gains of the responses have much significance. In different experiments, the only consistent features were the lower

FIGURE 31.

Plot of closed loop responses of a crab to 2° ramp movements of a striped drum at different velocities. The responses are plotted as a percentage of the stimulus. For comparison, the response of the same crab to a 2° memory stimulus (dark period 3 secs) under closed loop conditions is also shown. The vertical lines represent standard deviations from the means of between 4 and 20 responses. When vertical lines are absent, the point on the graph represents a single response.


100
90
80
70
60
50
40
30
20
10
0
% RESPONSE
0·001
0·01
0·1
1
10
RAMP VELOCITY %/sec
memory
stimulus

gain of memory responses compared to all ramp responses and, less consistent, the lower gain of step responses (4°/sec ramps) compared to slower ramp responses.

Unlike the responses obtained by Horridge and Sandeman (1964) to continuous constant velocity movement of a striped drum in which the gain of the eye responses to drum velocities above 0.5°/sec was low, the responses to ramp stimuli never fell below a mean of 55% of the stimulus. There were two main reasons for this. First, step and ramp responses, as discussed above, have a memory component, so the gain of the responses never falls below that of memory. Second, as illustrated in Fig. 12, the initial gain of the response to a fast movement is relatively high and it is only after $1-2^{\circ}$ of movement that the response adapts to a low level. Thus ramp stimuli illustrate the unadapted velocity response of the eye with its associated memory component, while continuous drum movement illustrates the partially adapted velocity response of the eye.

As was described by Horridge and Sandeman (1964), the gain of the responses of most crabs fell off when the drum velocity was lowered below 0.005°/sec. However, the responses of one crab (plotted in Fig. 33) showed no decrease, even at a ramp velocity of 0.00062°/sec, the lowest velocity possible with the apparatus used. This velocity is less than one sixth of the speed of the sun across the sky, demonstrating that the lower limit of the optokinetic response is extraordinarily low in some crabs.

In the memory situation, Carcinus shows a directional response to a movement of 1° after a dark period of up to 15 minutes (Horridge and Shepheard, 1966). This movement is equivalent to a velocity of $0.001^{\circ}/\text{sec}$ and is thus of the same order as the lower limit of the ramp responses described above. Also, the presence of eye tremor necessitates the averaging of low velocity stimuli over several seconds before movement can be deduced. Thus it is probable that all responses to slow drum movements are memory responses.

These experiments have shown that optokinetic memory, far from being an isolated phenomenon occurring only when the drum movement is not seen by the crab, plays an integral part in most of the optokinetic responses of the eye.

6) INTERACTION BETWEEN THE EYES.

Most of the experiments described so far in this thesis have involved recording the movements of only one of the eyes of a crab. Yet crabs have two eyes and all effects of binocular vision have been ignored in these experiments. Horridge and Sandeman (1964), in their study of the optokinetic response of Carcinus, made the assumption that there was only one amplifier in the eye movement control system, and that this amplifier had inputs from and outputs to both eyes. They thus preducted that both eyes would be absolutely linked together for all visual responses. The following experiments were carried out to test (a) whether this was so, and (b) if not, what simple model would describe the linkage between the eyes of a crab.

Experiments in which the movements of both eyes of Carcinus were recorded simultaneously have given some indication that the eyes are not absolutely linked together for all movements. As shown in Fig. 4, the tremors of the two eyes were independent of each other in most crabs, and even in crabs where the dominant oscillation of the tremors of the two eyes were closely linked, smaller movements of the eyes were independent. Though the eyes sometimes flicked together (Fig. 5D), a saccade of one eye alone was a frequent occurrence (Fig. 5A). Similarly, drift and the eye scanning that accompanied leg waving occurred independently in the two eyes (Fig. 6B).

These observations do not, however, give any indication as to whether the optokinetic responses of the eyes are controlled by a single amplifier or whether each eye has its own amplifier, for the fact that nine different muscles are involved in the movements of each eye could account for a small degree of independence between the eyes.

Responses of the eyes when each eye viewed a different visual stimulus.

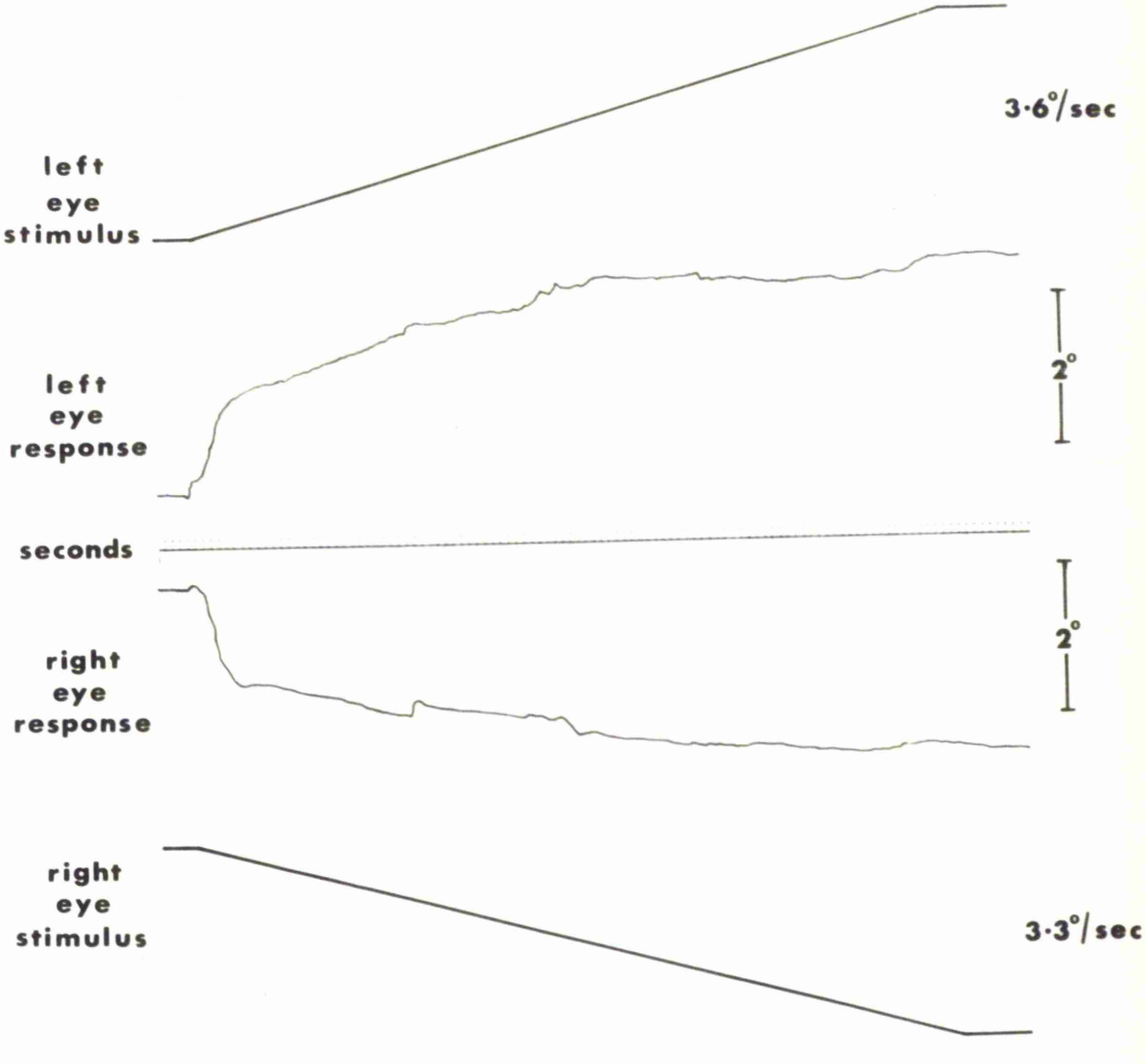
Qualitative results.

The simplest method of finding out whether or not the optokinetic responses of the two eyes were linked was to give each eye a different visual stimulus and observe whether the eyes moved independently of each other. In these experiments the crab was clamped at the centre of a large glass dish around which two loops of stripes could be moved independently of each other at a variety of different velocities (Fig. 2). The responses of both eyes were recorded simultaneously in the usual way.

When the two loops of stripes were moved in opposite directions at approximately equal velocities (Fig. 34), each eye initially followed the movement of its own stimulus. Therefore the optokinetic responses of the eyes are not absolutely linked and all descriptions of the eye movement control system in which both eyes are driven by a single amplifier are inapplicable. Each eye must have its own amplifier. Yet, as Fig. 34 shows, the eyes did not continue indefinitely to move in opposite directions. Therefore the eyes were not completely independent, but interacted in some way, so that after a time the two stimuli

FIGURE 34.

The responses of the two eyes when each eye saw a different set of stripes. In this record the two loops of stripes were moving in opposite directions at approximately equal velocities. Each eye initially followed the movement of its own stimulus, but after a few seconds slowed down and after c. 40 secs was more or less stationary. Movement to the right is shown by a downwards movement of the trace.


left eye stimulus
3·6°/sec
left eye response
2°
seconds
2°
right eye response
right eye stimulus
3·3°/sec

cancelled each other out and the eyes stopped moving.

This interaction between the eyes was worth examining in more detail. The two sets of stripes were thus moved in the same direction but at different velocities, the stripes seen by the left eye being moved much faster than those seen by the right eye. As can be seen in Fig. 35, the left eye initially responded much faster than the right eye, i.e. the eyes were initially independent as before. However, after about 30 secs., the left eye slowed down so that the two eyes were finally moving at about the the same velocity. It should be noted that the final velocity of both eyes was the initial velocity of the eye that saw the slower moving stripes.

When the two loops of stripes were not only moved at very different velocities but also in opposite directions, the eyes, as before, initially followed the movement of their own stimulus (Fig. 36). However, after a few seconds, the left eye, which observed the faster moving stripes, stopped moving and then moved slowly in the opposite direction at approximately the same velocity as the right eye. Notice again that it was the slower moving of the two stimuli that determined the direction and final velocity of both eyes, and that this took place even though the left eye, by doing so, moved in the opposite direction to the movement of the stripes it viewed. This response occurred irrespective of the directions of the eye movements relative to the crab's midline.

FIGURE 35.

The responses of the two eyes when each eye saw a different set of stripes. In this record the two loops of stripes were moving in the same direction at different velocities. Initially, the left eye, which observed the faster moving stripes, moved faster than the right eye. However, after c. 30 secs, it slowed down so that the two eyes ended up responding at about the same velocity. Movement to the right is shown by a downwards movement of the trace.

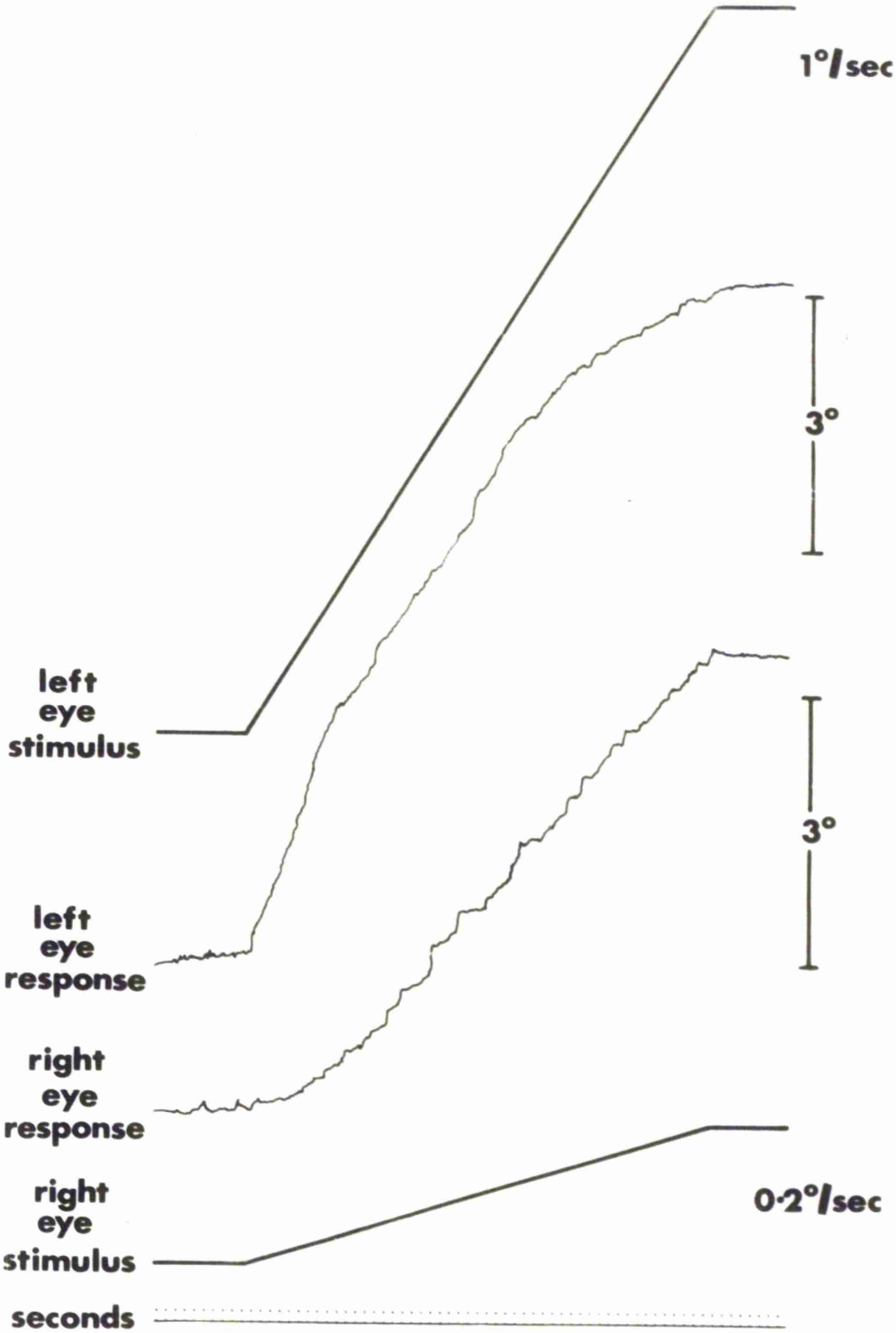
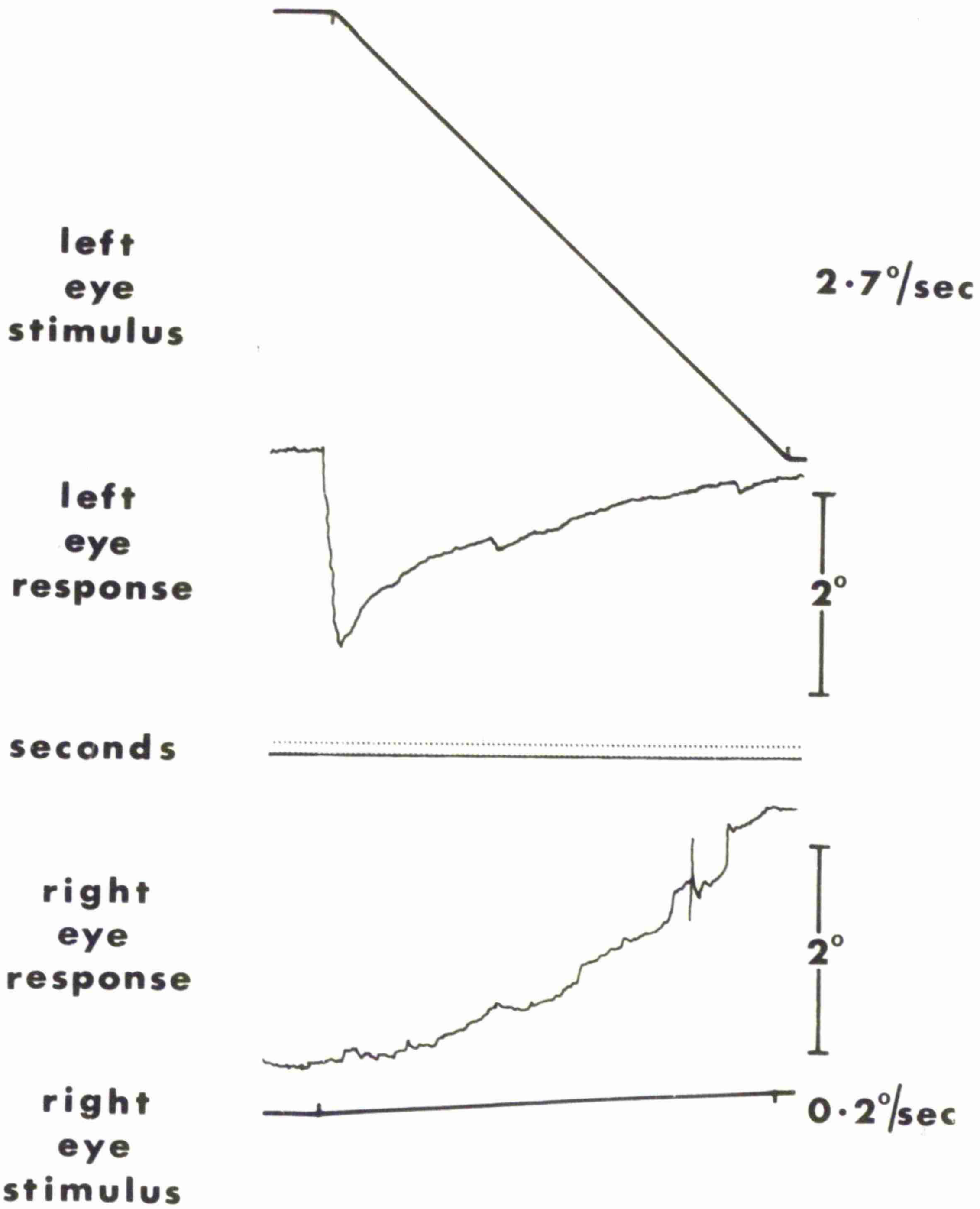

1°/sec
3°
left
eye
stimulus
3°
left
eye
response
right
eye
response
right
eye
stimulus
0·2°/sec
seconds

FIGURE 36.

The responses of the two eyes when each eye saw a different set of stripes. In this record the two loops of stripes were moving in opposite directions at different velocities. Each eye initially followed the movement of its own stimulus. However after a few seconds, the left eye, which observed the faster moving stripes, stopped moving and then moved slowly in the opposite direction at approximately the same velocity as the right eye. Movement to the right is shown by a downwards movement of the trace.


left eye stimulus
2·7°/sec
left eye response
2°
seconds
right eye response
2°
right eye stimulus
0·2°/sec

Horridge and Sandeman (1964) observed that an eye which viewed a moving striped drum did not respond if the other eye viewed a stationary set of stripes. Since in the above experiments, the eyes initially followed the movements of the stripes they viewed, Horridge and Sandeman's experiment was repeated using the apparatus illustrated in Fig. 2. As shown in Fig. 37, both eyes initially responded to the movement seen by the right eye, the right eye at the greater velocity. However, after two minutes, when the eye seeing the moving stripes had moved through 3°, the other eye rather less, both eyes had slowed almost to a standstill. This result, though different from that obtained by Horridge and Sandeman, is in accord with those described above, for the eyes initially showed partial independence and the final velocity of both eyes (zero) was the velocity of the slower of the two stimuli. The only difference between this and the previous results was that the eye seeing stationary stripes initially followed the stimulus to the other eye, albeit slowly, whereas in the previous experiments both eyes had initially responded to the stripes they viewed. Thus stationary stripes must initially have less influence in the determination of an eye's response than moving stripes.

In none of these experiments did both eyes follow the faster of the stimuli to the two eyes when both were moving in opposite directions. Such a response could, however, be induced if the fast movement of the stripes seen by one eye began several seconds after the slow movement of the stripes facing the other eye. As shown in Fig. 38, the right eye, which viewed the slower moving stripes, changed the direction of its

FIGURE 37.

The responses of the two eyes when each eye saw a different set of stripes. In this record the left eye faced a stationary set of stripes, while the right eye saw moving stripes. Both eyes initially responded to the moving stripes, the right eye at the greater velocity. However, after c. 2 mins, both eyes had slowed down and were more or less stationary. Movement to the right is shown by a downwards movement of the trace.

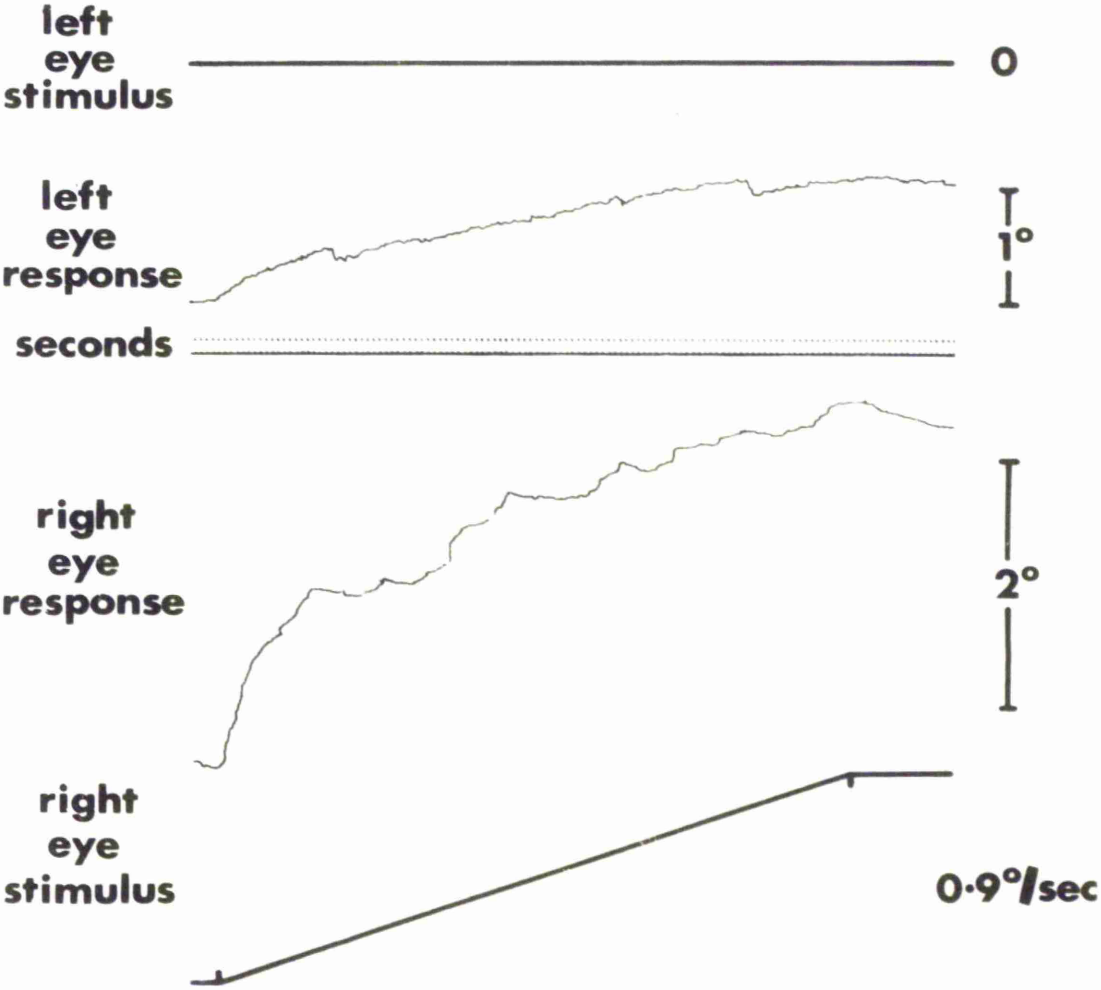

left eye stimulus
0
left eye response
1°
seconds
right eye response
2°
right eye stimulus
0·9°/sec

FIGURE 38.

The responses of the two eyes when each eye saw a different set of stripes. In this record the stimulus sequence was as follows:-

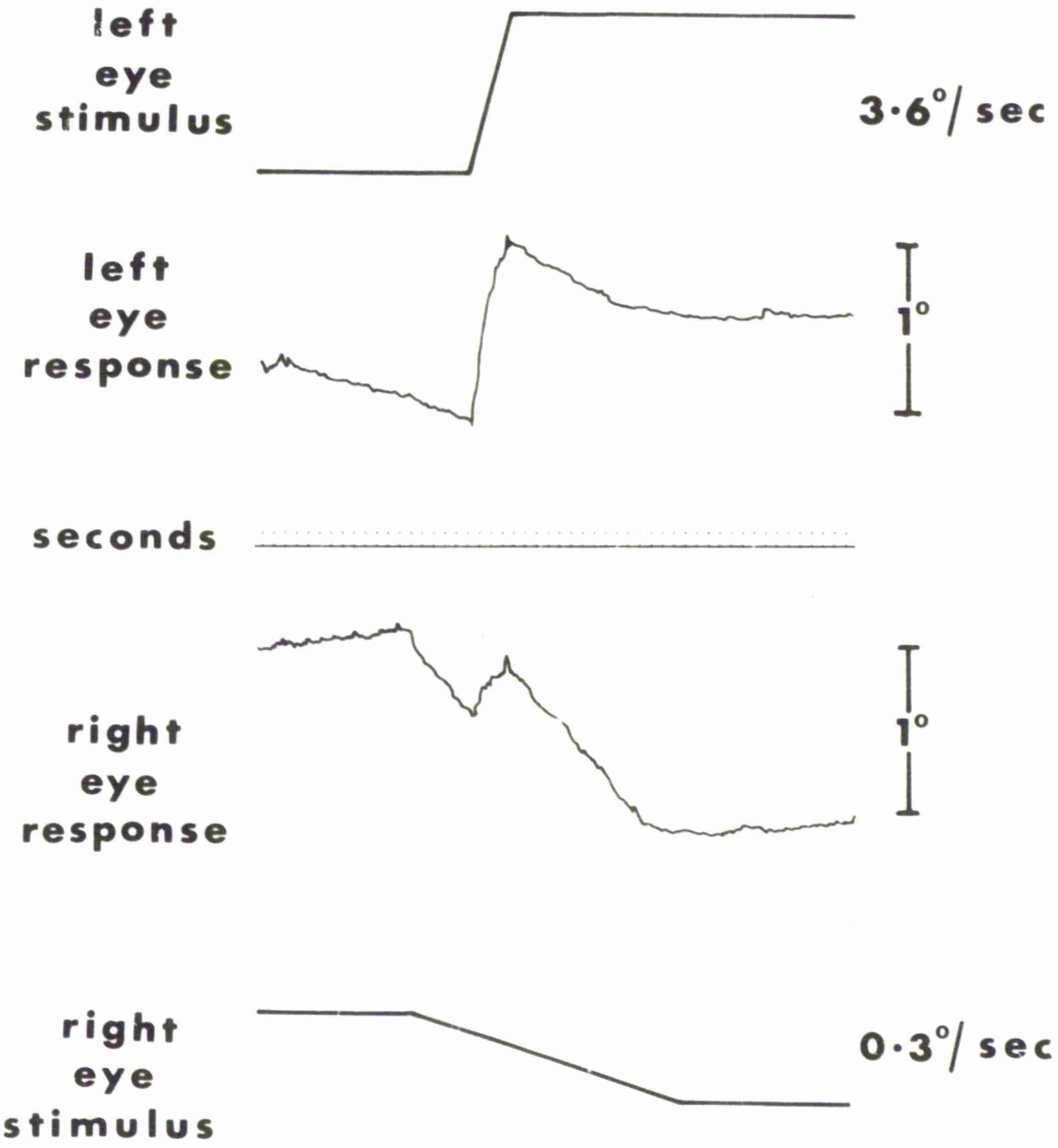
i. Right eye stimulus started to move to the right at 0.3°/sec.

ii. After 6 secs, left eye stimulus started to move to the left at 3.6°/sec.

iii. 3 secs later, left eye stimulus stopped moving.

iv. Finally after a further 15 secs, the right eye stimulus stopped moving.

This is the only experimental situation in which an eye followed the stimulus to the other eye, when the stimulus to the other eye was faster than its own stimulus (this excludes the consideration of stationery stripes). Movement to the right is shown by a downwards movement of the trace.


left eye stimulus
3·6°/sec
left eye response
1°
seconds
right eye response
1°
right eye stimulus
0·3°/sec

response when the stripes facing the other eye began to move. As would be predicted from previous experiments, the left eye did the same, so for a time both eyes followed the faster of the two visual inputs. This apparently contradictory result is best explained by considering the faster stimulus as a novel stimulus since it began several seconds after the slower stimulus to the other eye. Because of this, the left eye movement detector had considerably more influence over the right eye control system than it would under normal conditions.

From these different experiments, some general conclusions can be drawn. Each eye must have its own system for converting perceived motion into eye movement. These two systems are not completely independent of each other but show a certain amount of interaction. Initially the eyes move more or less independently, but after a few degrees of movement, the eyes either come to a standstill or move in the same direction at more or less the same velocity. Stationary or slow moving stripes take precedence over fast moving stripes in that the final velocity and direction of the movement of both eyes is determined by the slower of the two visual inputs. There are only two situations in which an eye will follow, even for only a few seconds, a faster stimulus to the other eye. These are (a) when the eye is facing a stationary set of stripes and (b) when the stimulus to the other eye is a novel one.

Quantitative results.

The above description is, however, limited in that it is purely qualitative. Some quantitative measure of the interaction between the eyes is desirable.

The velocity of the movements of the two eyes was thus measured and plotted against the velocity of the stimulus to one of the eyes. The stimulus to the other eye was kept constant so that only one stimulus variable was changed at a time. However, as is illustrated in Figs. 34-37, the eyes do not move at constant velocity. Two different measurements were thus made of the velocity of an eye's response. These were (a) its initial velocity and (b) its final velocity. From these graphs, the interaction between the eyes, both at the start and at the finish of a response, could be easily assessed.

In all experiments from which these measurements were made, the movements of the two loops of stripes were always initiated at the same time. This avoided all responses due to novel stimuli. Although responses occurring in different directions were separated from each other in different graphs, no differences could be observed between responses occurring towards and away from the crab's midline.

Fig. 39 shows the initial velocities of the responses of the two eyes when the stimulus to the left eye was a movement of the stripes to the left at a constant velocity of 0.95°/sec. It had been concluded from the qualitative results described earlier that the eyes moved more or less independently of each other during the initial part of a response. However, this conclusion is not entirely valid, for Fig. 39 shows that the

FIGURE 39.

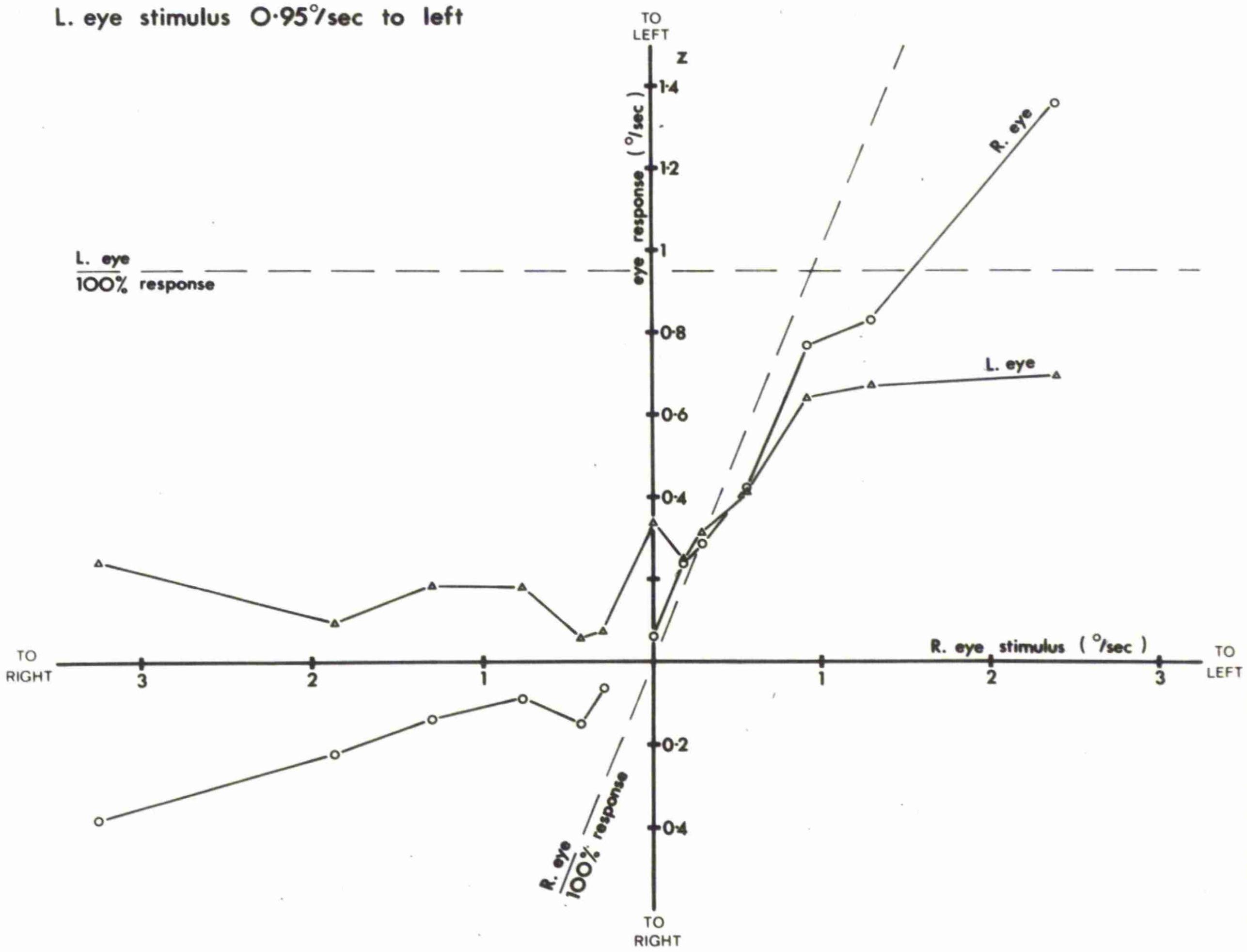
The initial velocities of the responses of the two eyes when each eye saw a different set of stripes.

Y-axes - initial velocity of the eye responses in degrees / sec. Responses to the left are plotted above the X-axis, those to the right below the X-axis.

X-axes - velocity of the stimulus (moving stripes) to the right eye in degrees / sec. Movement to the left is plotted on the right of the Y-axis, that to the right on the left of the Y-axis.

The stimulus to the left eye (moving stripes) was constant at a velocity of 0.95°/sec. to the left.

Each point on the graph is the mean of up to 5 responses, all responses being from the same crab. Theoretical lines representing 100% responses of the two eyes are drawn on the graph for comparison with the actual responses.


L. eye stimulus 0·95°/sec to left
TO LEFT
Z
1·4
1·2
1
0·8
0·6
0·4
eye response (°/sec)
R. eye
L. eye
100% response
L. eye
TO RIGHT
3
2
1
1
2
3
R. eye stimulus (°/sec)
TO LEFT
0·2
0·4
R. eye
100% response
TO RIGHT

eyes interacted to some extent. Certainly the eyes initially responded in the direction of the movement of the stripes they viewed. However, the velocity of the initial part of an eye's response was far from independent of the velocity and direction of movement of the stimulus to the other eye.

This interaction is illustrated best by the left eye responses of Fig. 39. Since the stimulus to the left eye was constant at 0.95°/sec. the initial velocity of the left eye response would have been constant at some value between 0.5°/sec. and 0.8°/sec, irrespective of the stimulus to the right eye, if the eyes had been independent of each other. However, the left eye only responded at a velocity above 0.5°/sec when the stimulus to the other eye was a movement of the stripes in the same direction at a velocity between 0.7°/sec and 2.4°/sec. If the stripes viewed by the other eye were moving slower than this, were stationary, or were moving in the opposite direction, the left eye response was much reduced. This reduction was greatest when the stripes viewed by the other eye moved in the opposite direction at a velocity between 0.2°/sec and 0.7°/sec. Under these conditions, the initial velocity of the left eye response was less than 0.2°/sec.

This interaction between the eyes did not only involve reduction in an eye's response. For instance, the initial velocity of the right eye response of Fig. 39 was sometimes greater than the velocity of the stripes it viewed. This occurred when the right eye stimulus velocity was less than one third of the left eye stimulus velocity and both loops of stripes were moving in the same direction.

In some crabs, the degree of interaction between the eyes during the initial part of a response was much greater than this. The two graphs that follow, Figs. 40 and 41, illustrate the initial velocities of the eye responses of two crabs that show close interaction between the eyes. In Fig. 40, the stimulus to the left eye was a movement of the stripes to the left at a constant velocity of 0.95°/sec. The experiment was thus identical to that illustrated in Fig. 39. The responses were, however, different in two respects. Firstly, when the stimuli to the two eyes were moving in opposite directions, the velocities of the responses were reduced far more than were those in Fig. 39, and few responses occurred at a greater velocity than 0.1°/sec. Secondly, when the two loops of stripes were moving in the same direction but at different velocities, both eyes nevertheless moved at approximately the same velocity. This degree of linkage between the eyes was not observed at the start of a response in most crabs.

In Fig. 41, the stimulus to the left eye was a movement of the stripes to the right at a constant velocity of 2.74°/sec. The significant feature of this figure is the interaction between the eyes that occurred when the two loops of stripes were moving in opposite directions at different velocities. In this situation, the eyes of most crabs initially responded in the direction of movement of the stripes they viewed as shown in Fig. 36. However, in this crab, both eyes responded in the direction of the stimulus to the right eye when the

FIGURE 40.

As Fig. 39 but for a different crab. Unlike Fig. 39 where the eyes were relatively independent of each other during the initial part of a response, the responses of Fig. 40 show that there is close interaction between the eyes in some crabs. For instance, when the stimuli to the two eyes were moving in opposite directions, the velocities of the responses were reduced far more than were those in Fig. 39. Also, when the two loops of stripes were moving in the same direction but at different velocities, both eyes nevertheless moved at approximately the same velocity.

L. eye stimulus 0·95°/sec to left

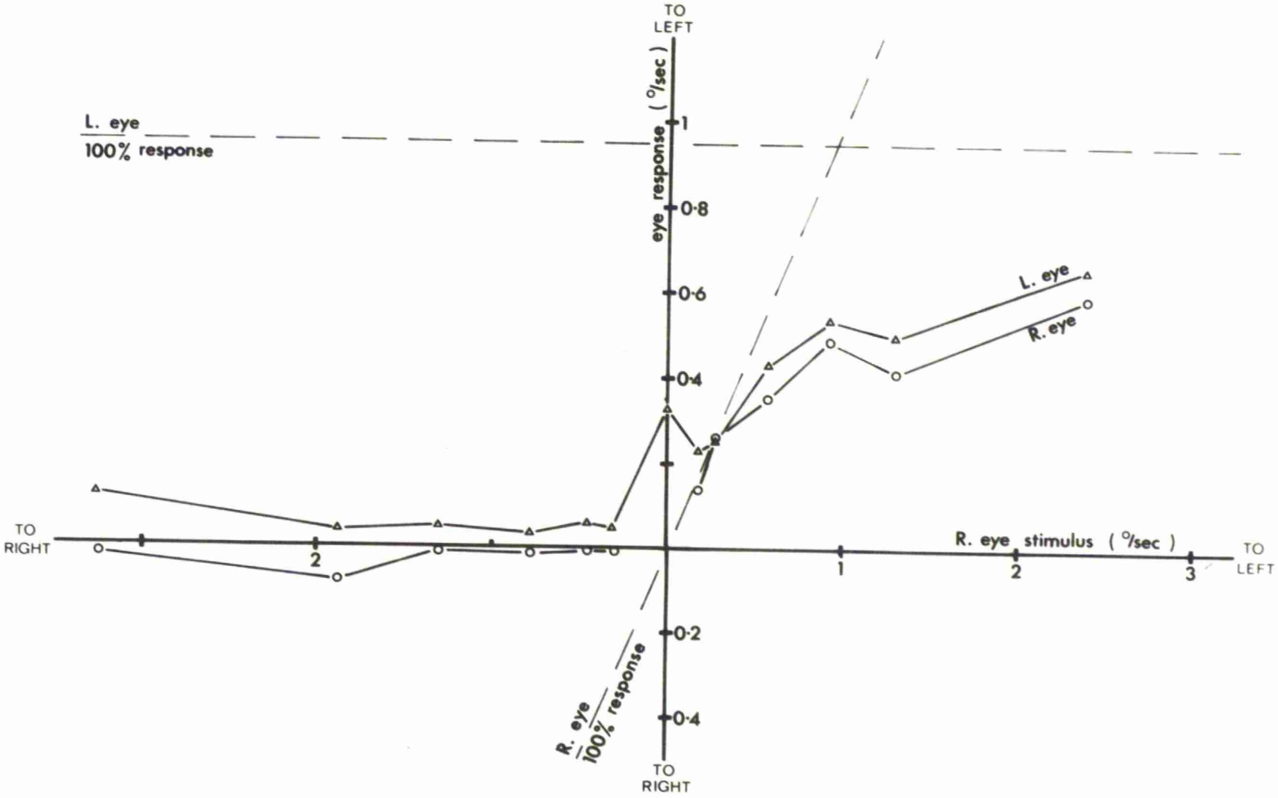
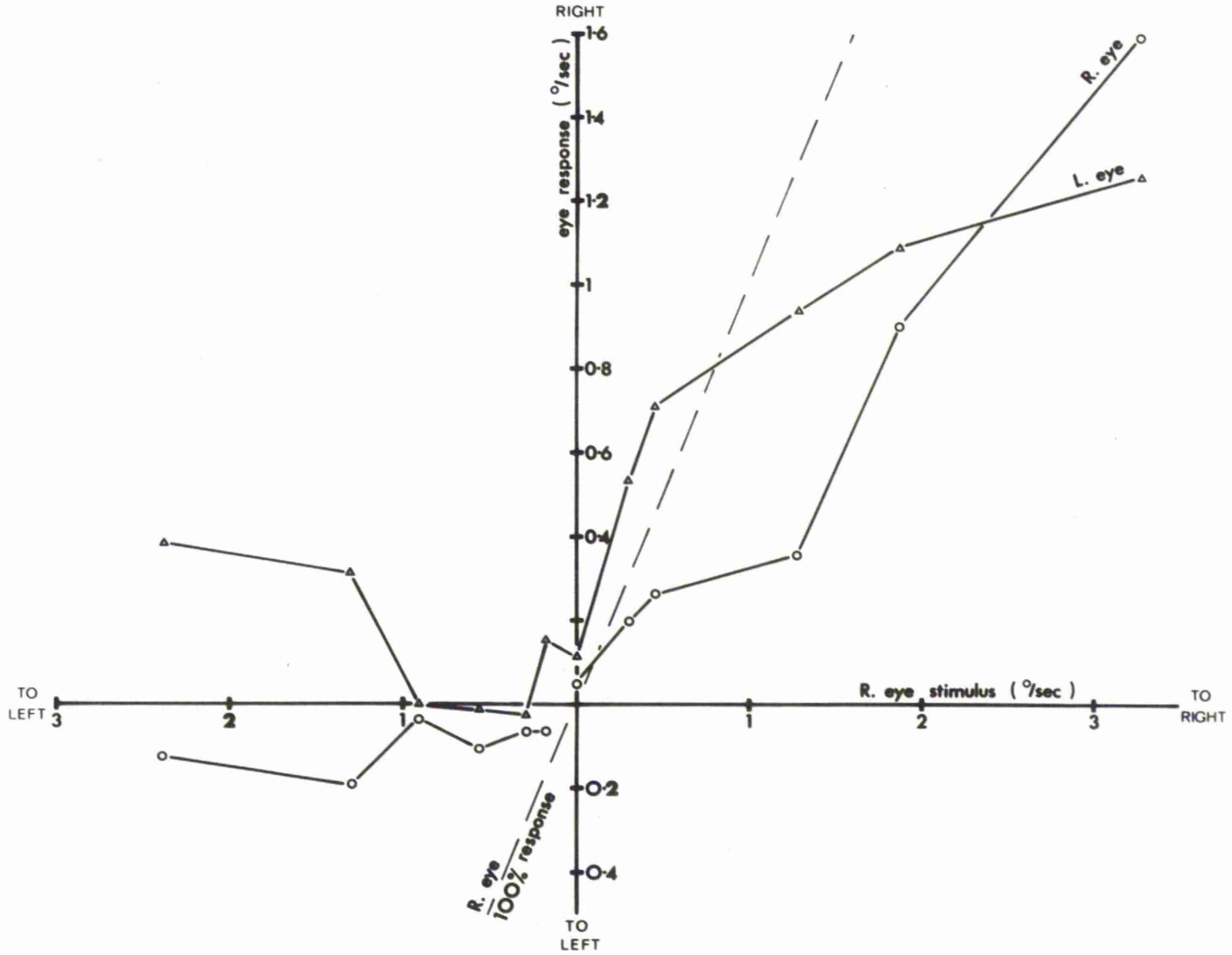


FIGURE 41.

As Fig. 39 but left eye stimulus 2.74°/sec to the right. In order to make the graph directly comparable with Fig. 39, stimuli moving to the left were plotted on the left of the Y-axis, those to the right on the right of the Y-axis. Responses to the left were plotted below the X-axis, those to the right above the X-axis.

Note that, unlike the eyes of most crabs which initially responded in the direction of the stripes they saw, the left eye initially responded in the direction of movement of the stripes seen by the right eye when the two sets of stripes were moving in opposite directions at different velocities.

L. eye stimulus 2·74°/sec to right



latter was moving to the left at a velocity between 0.3°/sec and 0.9°/sec. This degree of interaction between the eyes at the start of a response, involving the direction of the response as well as its quantitative output/input ratio was not found in any other crab.

Whatever the initial interaction between the eyes, the eyes became less independent as the responses progressed. This change was a gradual one taking between twenty seconds and five minutes. It resulted, as discussed earlier, in the eyes either coming to a standstill, or moving in the same direction, often at similar velocities.

The velocities of the responses of the two eyes when the above changes had taken place are shown in Fig. 42, the two graphs representing the responses of two different crabs.

When the two loops of stripes were moving in opposite directions at approximately equal velocities, the final velocity of all responses was zero. This occurred in Fig. 42A when the right eye stimulus was a movement of the stripes to the left at a velocity below 1°/sec, and in Fig. 42B when the stripes seen by the right eye moved to the left at a velocity above 2°/sec. Both eyes had slowed to a halt. The angle through which the eyes moved and the time the eyes took to come to a halt depended to some extent on the stimulus velocity. When the stimuli to the two eyes moved at velocities between 0.2°/sec and 1°/sec, the eyes came to a standstill in a mean of 70 secs after moving through a mean of 2.5°. These values were decreased to 55 secs and 2°

FIGURE 42.

The final velocities of the responses of the two eyes when each eye saw a different set of stripes.

Y-axes - final velocity of the eye responses in degrees/sec. Responses to the left are plotted below the X-axis, those to the right above the X-axis.

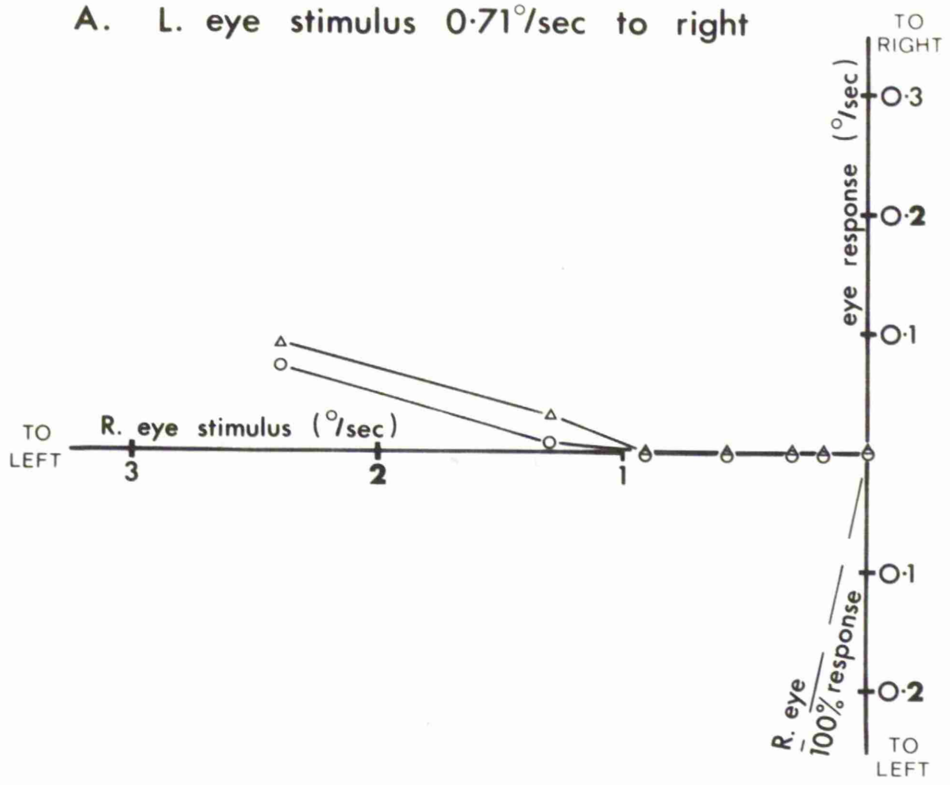
X-axes - velocity of the stimulus (moving stripes) to the right eye in degrees/sec. Movement to the left is plotted to the left of the Y-axis.

In A, the stimulus to the left eye (moving stripes) was constant at a velocity of 0.71°/sec to the right; in B it was constant at 2.74°/sec to the right.

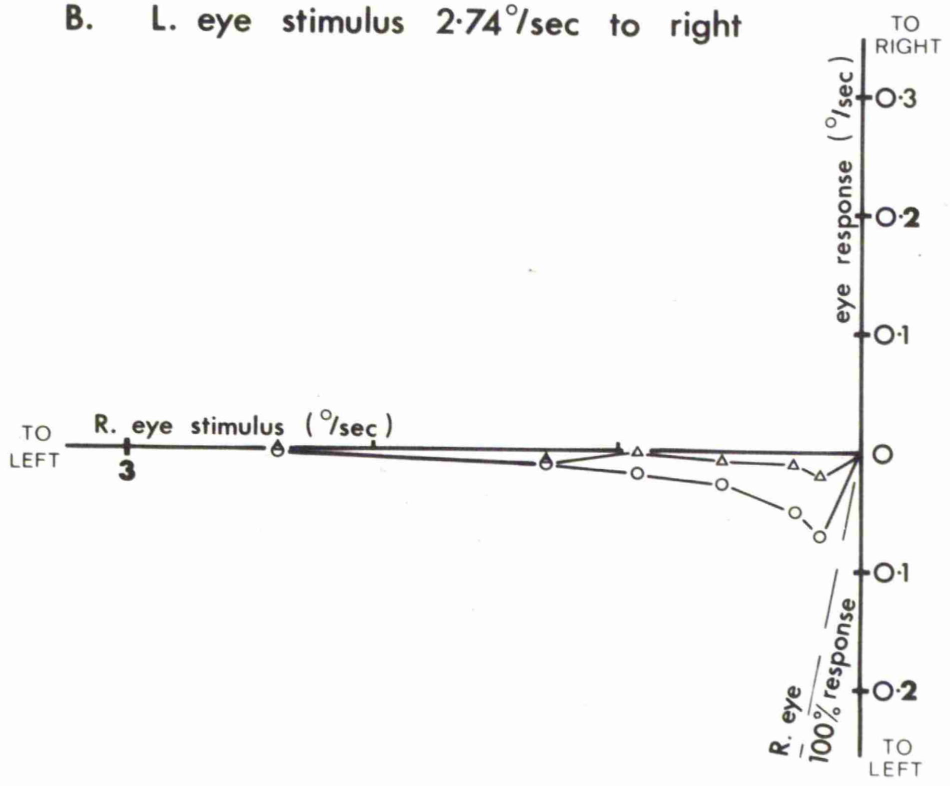
Each point on the graph is the mean of up to 5 responses, the two graphs being the responses of different crabs.

o - right eye responses.

△ - left eye responses.



A. L. eye stimulus 0·71°/sec to right



B. L. eye stimulus 2·74°/sec to right

respectively when the stimulus velocities were increased to between 2.4°/sec and 3.4°/sec. The final velocities of the eye responses only took up values other than zero when the two loops of stripes were moving in opposite directions, if the velocity of the stimulus to one eye was at least twice as great as that to the other eye. Figs. 42A and B show that both eyes finally responded in the direction of movement of the slower moving stripes, and that the velocity of these responses seldom exceeded 0.1°/sec. The eye viewing the faster moving stripes had thus slowed to a standstill, and had then begun to move in the opposite direction, though usually at a lower velocity than the other eye. This change of direction usually occurred about 20 secs after the start of a response, the eye having previously moved through a mean of 2.2°.

When the two loops of stripes were moving in the same direction, it was difficult to observe to what extent the eyes maintained their initial partial independence because of the periodic intervention of fast phases. However, it will be shown in Section 7 of the "Results" that fast phases to the left are initiated by the left eye control system and fast phases to the right by the right eye control system. The interval between successive fast phases to the left and right may thus be used as a measure of the velocity of, respectively, the left and right eye responses. Figs. 43 and 44 therefore give an indication of the degree of interaction between the eyes when both loops of stripes were moving in the same direction at different velocities.

Most crabs gave responses similar to those shown in Fig. 43. In this graph, the interval between fast phases to the left was affected

FIGURE 41.

The mean interval between successive fast phases during an experiment in which each eye saw a different set of stripes. Both sets of stripes were moving in the same direction but at different velocities. Each point on the graph is the mean of up to 12 responses.

X-axis - velocity of the stimulus (moving stripes) to the right eye in degrees/sec.

Y-axis - mean interval between successive fast phases in seconds.

△ - velocity of stimulus to left eye 0.75°/sec.

o - velocity of stimulus to left eye 3.00°/sec.

Curves connecting the points on the graph were drawn by hand.

Note that changes in the velocity of the stimulus to both right and left eyes caused changes in the interval between successive fast phases.

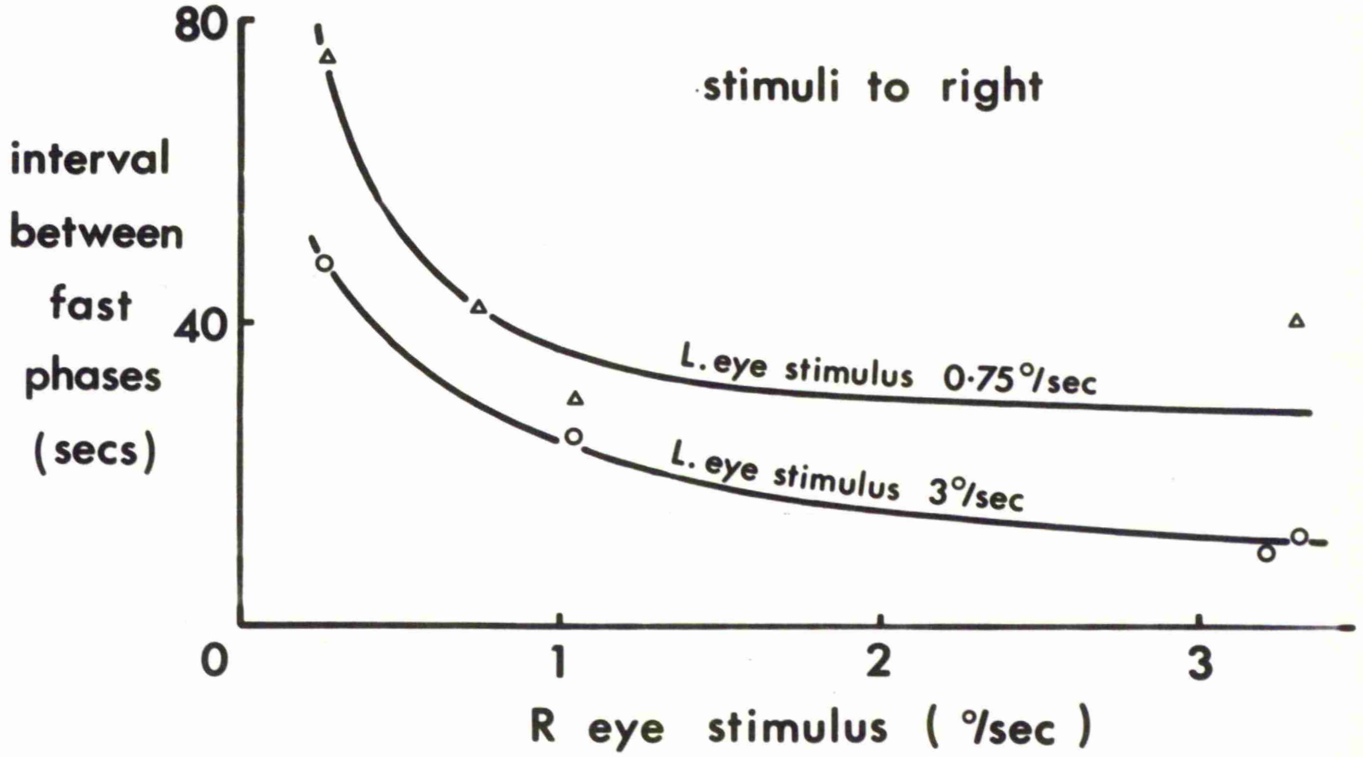
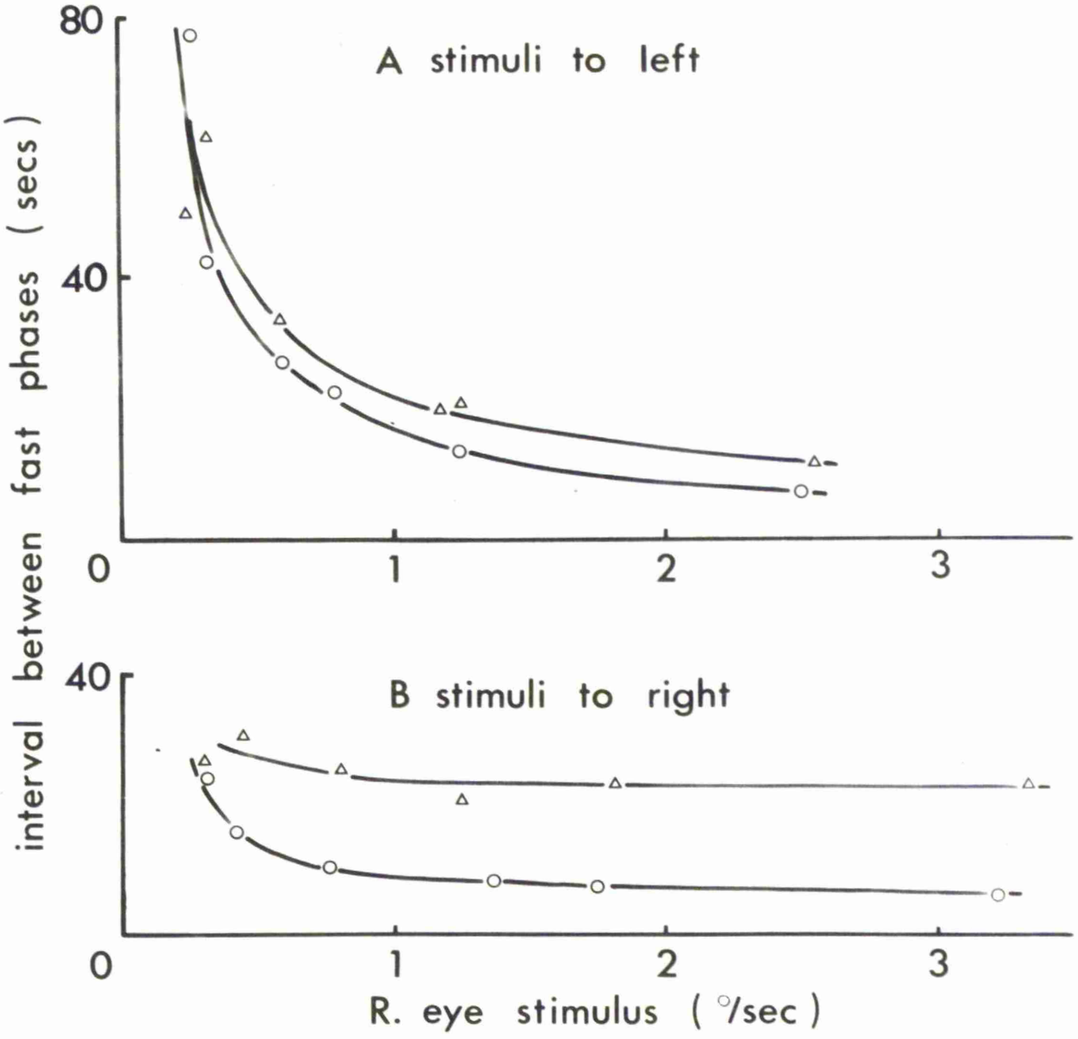

80
40
0
interval between fast phases (secs)
stimuli to right
L. eye stimulus 0·75°/sec
L. eye stimulus 3°/sec
1
2
3
R eye stimulus (°/sec)

FIGURE 44.

As Fig. 43 but a different crab. The upper graph shows the results obtained when the stripes were rotated in an anti-clockwise direction, the lower graph, the results obtained when the stripes were rotated in a clockwise direction.

Unlike Fig. 43 where changes in the velocity of the stimulus to right and left eyes had approximately equal effects, the effects of these stimulus changes in this crab depended upon the direction of rotation of the stripes. During movement of the stripes to the left, the interval between fast phases was altered more by changes in the right eye stimulus velocity than by changes in the left eye stimulus velocity. During movement of the stripes to the right, the interval between fast phases was affected most by changes in the left eye stimulus velocity.


80
40
0
A stimuli to left
1
2
3
40
0
B stimuli to right
1
2
3
interval between fast phases (secs)
R. eye stimulus (°/sec)

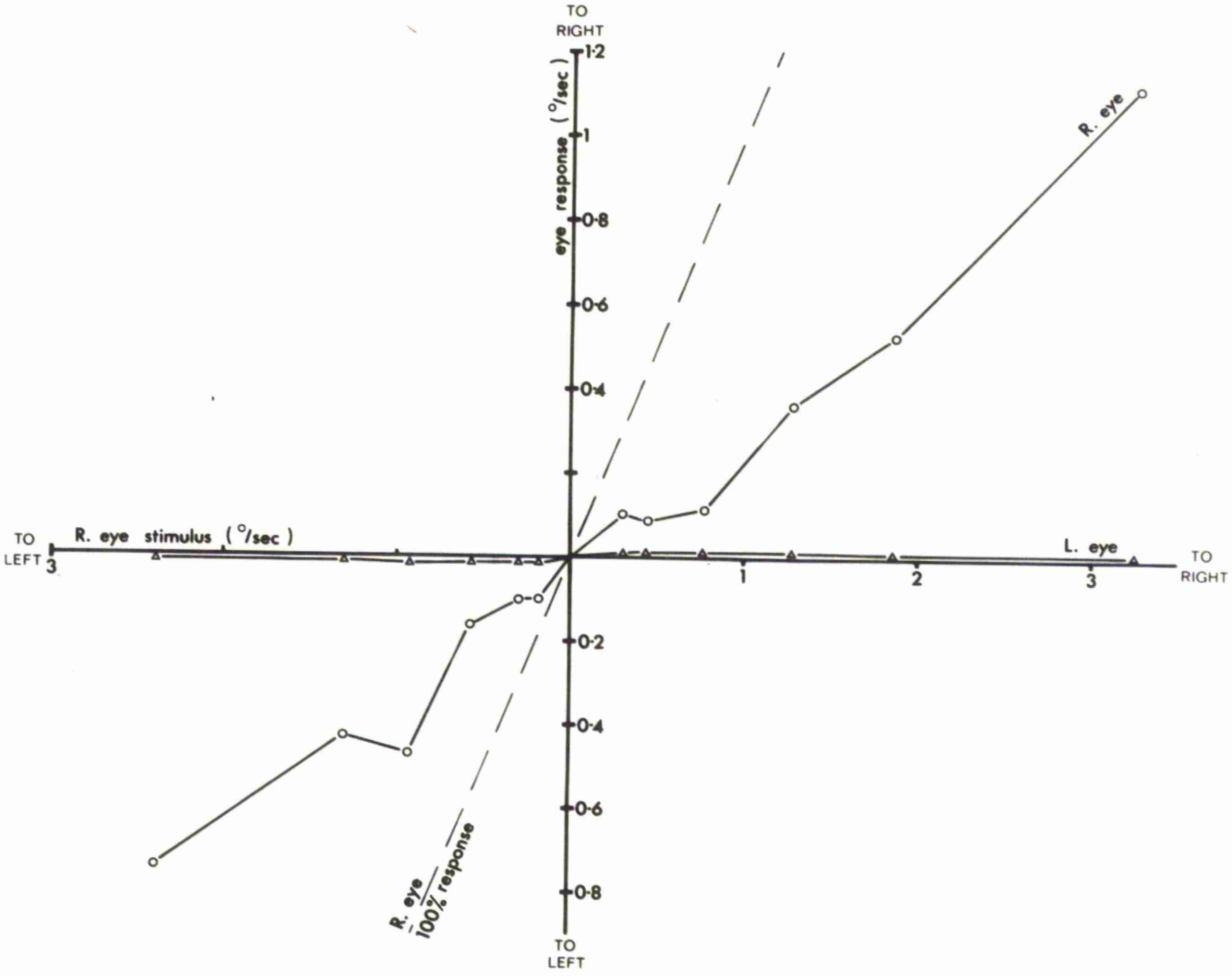
equally by changes in the stimulus to either eye. From this it was deduced that the left eye velocity was affected equally by velocity changes in either of the two loops of stripes, an indication that the eyes had little independence at this stage of the responses. In one crab, however, whose responses are plotted in Fig. 44, the interval between successive fast phases to the left was hardly affected by changes in the stimulus to the right eye, and the interval between fast phases to the right was hardly affected by changes in the stimulus to the left eye. In this crab therefore, an eye's response was substantially unaffected by changes in the stimulus to the other eye. This degree of maintained independence of the two eyes was not found in any other crab.

Since the results obtained from experiments in which one loop of stripes remained stationary differed slightly from those obtained by Horridge and Sandeman (1964), further quantitative measurements were made to check their validity. A graph of the initial velocities of the responses of both eyes of one crab is shown in Fig. 45. The graph confirms that both eyes responded to the movement seen by one eye, the eye seeing the movement at a velocity of approximately 30% of the stimulus, the other eye very slowly. Both eyes, as described earlier, slowed to a standstill. This occurred after about five minutes, the eye viewing the moving stripes having moved through up to 11°, the other eye through up to 6°. These are the values for stimulus velocities in the range of 0.3°/sec to 1°/sec. Increasing the stimulus velocity caused a reduction in the response, the eyes moving through means of 4° and 1°

FIGURE 45.

As Fig. 39, but left eye viewed a stationary set of stripes. The line representing a 100% response of the left eye is thus the X-axis.

Figs. 39 and 45 represent the responses of the same crab, whose eyes were initially relatively independent of each other.


TO RIGHT
1·2
eye response (°/sec)
1
0·8
0·6
0·4
R. eye
TO LEFT
3
R. eye stimulus (°/sec)
L. eye
1
2
3
TO RIGHT
0·2
0·4
0·6
0·8
R. eye
100% response
TO LEFT

respectively, and slowing to a halt within two minutes.

These quantitative measurements have thus substantially verified the qualitative results described earlier. They confirm that each eye has its own amplifier and that these amplifiers interact with each other. They show that the interaction between the eyes can take a variety of different forms and that the degree of interaction varies considerably in different crabs. In spite of this however, it has been generally found that the eyes interact with each other to only a small extent at the start of a response, and that the degree of interaction increases as the response progresses until the movements of the eyes are quite closely linked.

Memory and oscillation.

It was proposed in section 4 of "Results" that the stimulus to the crab in the memory situation was the mismatch between the present position of the stripes on the retina and a spatially remembered version of their previous position. This mismatch was presumed to be differentiated to velocity and fed into the control system for following optokinetic responses. If this is so, then the two eyes of a crab should interact with each other similarly for both pure velocity and pure memory stimuli, since both velocity and memory signals are presumed in the above hypothesis to be sent along the same information channels.

In the following experiments, the interaction between the eyes during memory responses, during the responses to 0.4 c.p.s. sinusoidal oscillation of the two loops of stripes, and during the responses to step functions, are compared.

Memory responses of the two eyes when each eye saw a different set of stripes are shown in Fig. 46. In these records, the two loops of stripes were moved independently of each other during short periods of darkness.

Both loops of stripes were first moved in the same direction through 2.3° as in a normal closed loop memory experiment. Trace A shows that both eyes responded in the direction of the movement of the stripes, the left eye response being 28% of the stimulus, the right eye response 16%. These responses are thus of lower than average gain. The loops of stripes were next moved in opposite directions through the same angle. As shown in trace B, both eyes responded <u>in the direction of the movement of the stripes they viewed</u> showing that, in the memory situation, the eyes have a considerable degree of independence. The responses were, however, reduced in amplitude, the left eye response being 12% of the stimulus, the right eye response 14%. Finally, only one loop of stripes was moved, while the other remained stationary. Trace C shows that both eyes responded in the direction of movement of the stripes, the response of the eye facing the stripes which had moved being 10-12% of the stimulus, the other eye rather less. The interaction between the eyes in this situation was thus very similar

FIGURE 46.

Memory responses of the two eyes when each eye saw a different set of stripes. In this record the two loops of stripes were moved independently during short periods of darkness.

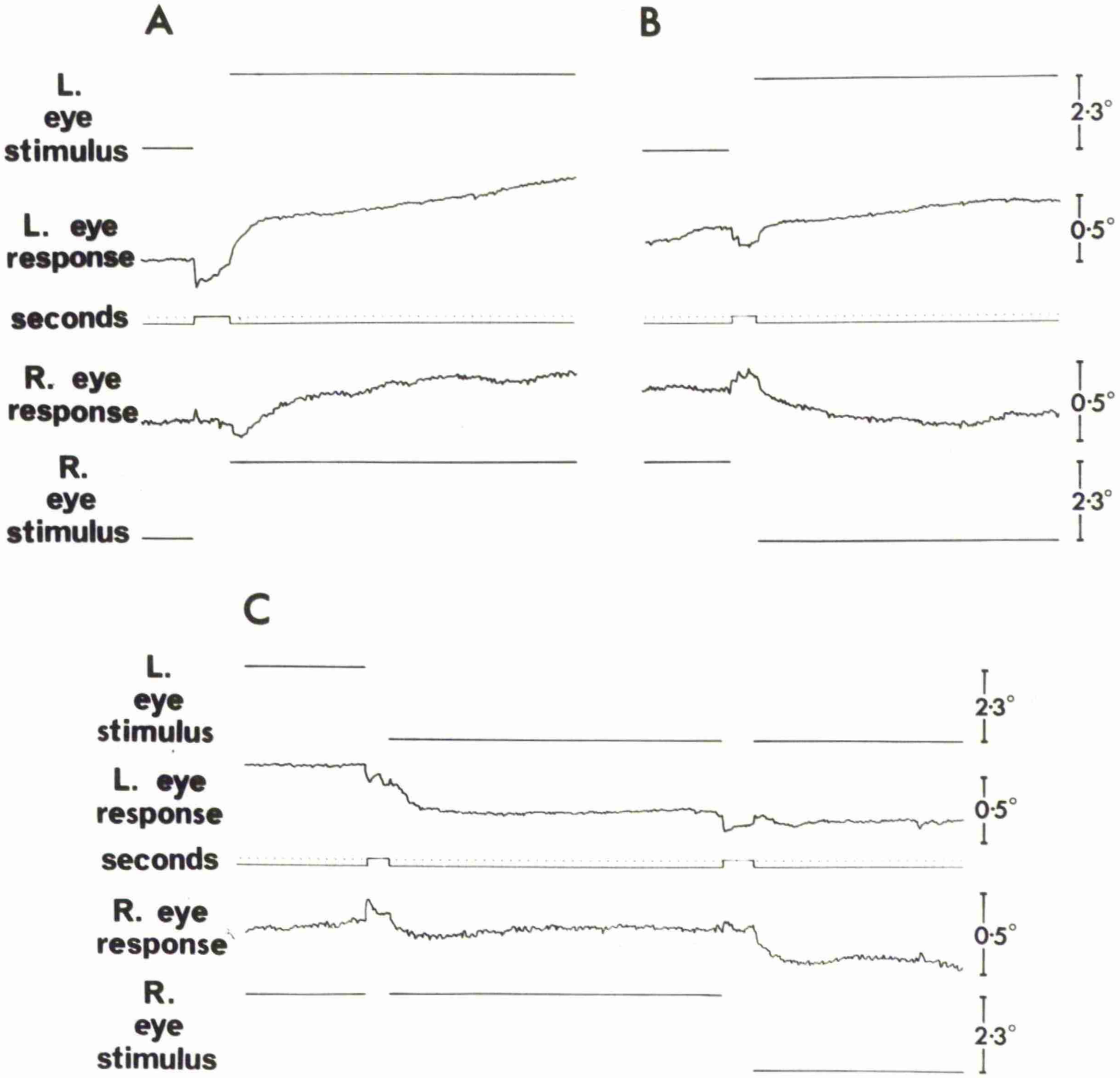
A. Both loops of stripes moved in the same direction through 2.3° as in a normal closed loop memory experiment.

B. The two loops of stripes moved in opposite directions through 2.3°.

C. One loop of stripes moved through 2.3°, the other remaining stationary.

The time trace is interrupted during the periods of darkness. Movement to the right is shown by a downwards movement of the trace.

Note that the eyes show a considerable degree of independence.


A
B
L. eye stimulus
2·3°
L. eye response
0·5°
seconds
R. eye response
0·5°
R. eye stimulus
2·3°
C
L. eye stimulus
2·3°
L. eye response
0·5°
seconds
R. eye response
0·5°
R. eye stimulus
2·3°

to that observed in Fig. 37. As all these responses took place when the stripes were stationary, the eyes must have perceived apparent motion occurring in the opposite directions to the eye's own movements and as a direct consequence of them.

The pure velocity stimulus used was 0.4 c.p.s. approximately, sinusoidal oscillation of the two loops of stripes. The responses illustrated in Fig. 47A are from the same crab as produced the memory responses described above. When both loops of stripes were oscillated in phase with each other, the left eye responded with an amplitude of 25-36% of the stimulus and the right eye with an amplitude of between 9 and 18%. Oscillation of the two loops of stripes 180° out of phase with each other caused the responses to be reduced to under 2% of the stimulus. The responses of the two eyes were however, <u>in phase with the oscillation of the stripes they viewed.</u> Resumption of in-phase oscillation resulted in an increase in the amplitude of the responses, but only to about one third of their initial value. Thus the influence of the conflicting input from the contralateral eye on the gain of the response is maintained even after its cessation. Apart from this, these velocity responses are similar to the memory responses described above, in that the direction of an eye's response depended on the direction of movement of the stripes it viewed. In both experiments, response amplitudes were reduced when the stimuli to the eyes were moved in opposite directions. This reduction was greater during velocity responses than during memory responses, but this was not unexpected since higher velocity eye responses always show greater adaptation than lower

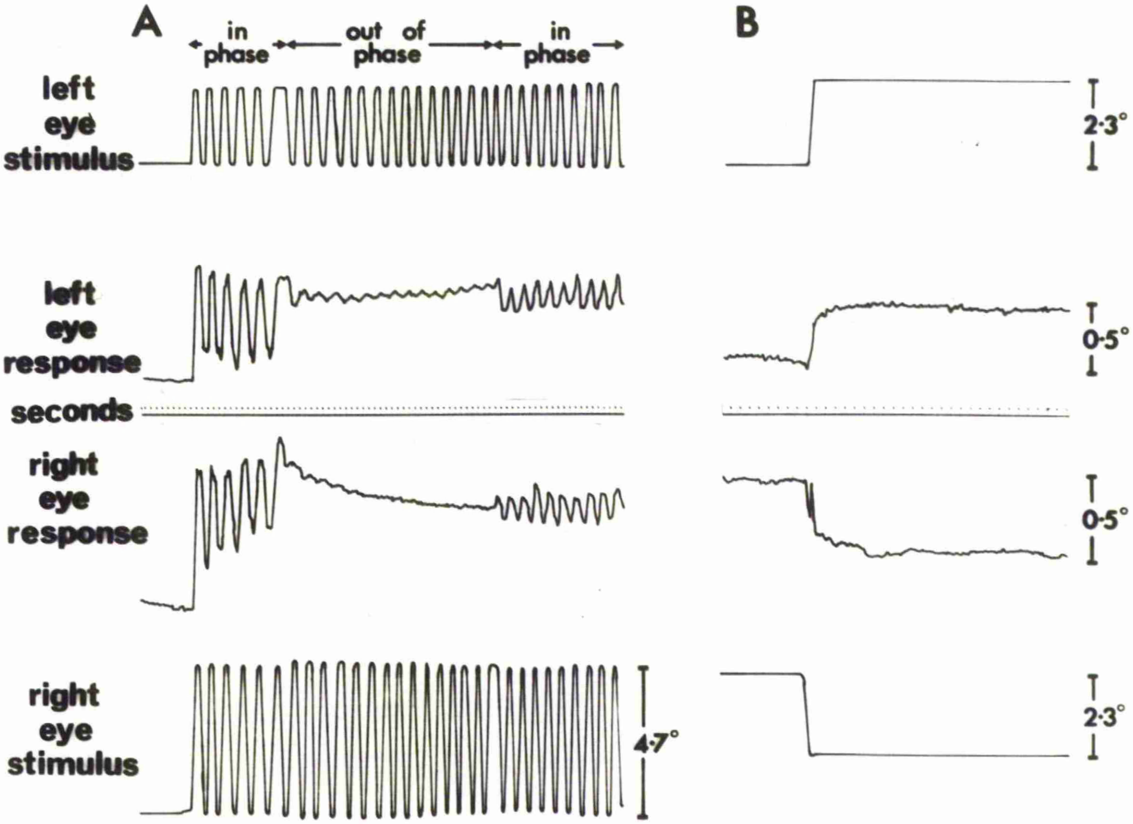
FIGURE 47.

Oscillatory and step responses of the two eyes when each eye saw a different set of stripes.

A. Oscillatory responses. The two loops of stripes were oscillated approximately sinusoidally at 0.4 c.p.s. both in phase and 180° out of phase with each other. Note that the out of phase responses, though small and adapting (at least in the right eye trace) were, when present, in phase with the movement of the stripes the eye saw. When the stripes were again oscillated in phase with each other, the responses were smaller than were the initial in phase responses.

B. Step responses. 2.3° step movements of the two loops of stripes in opposite directions induced independent responses from the two eyes, each in the direction of the step stimulus observed by that eye.

Movement to the right is shown by a downwards movement of the trace.


A
in phase
out of phase
in phase
left eye stimulus
left eye response
seconds
right eye response
right eye stimulus
4·7°
B
2·3°
0·5°
0·5°
2·3°

velocity ones (see Section 3 of the "Results").

A further check on the interaction between the eyes during velocity and memory experiments is given by the responses to step stimuli. As shown in Fig. 47B, both the velocity and memory components of the step responses were in the direction of the movement of the stripes they viewed. This confirms that the two eyes of a crab interact with each other similarly for both velocity and memory stimuli.

From this, it does not, of course, follow that both velocity and memory signals are necessarily sent along the same information channels. Rather it fails to prove the contrary hypothesis that velocity and memory signals are sent along different information channels.

Model describing the linkage between the eyes.

The above experiments have described in detail the interaction that occurs between the two eyes of a crab, but have given no indication as to where this interaction takes place. The following experiment was thus designed to show where, physiologically, this interaction occurred; i.e. whether the linkage between the eyes was on the sensory or the motor side of the brain. The experiment takes advantage of the fact, discovered by Sandeman (1964), that if one eye of a crab is blinded by painting it over with black paint, and a stimulus is given to the other eye, both eyes respond; i.e. the seeing eye drives the blinded eye. In this experiment the responses of both eyes to a standard visual stimulus to one eye (a 2° ramp function) were recorded, and a graph of blind eye responses against seeing eye responses plotted.

It has been shown that each eye has its own amplifier and that these amplifiers are linked. For crabs in the above situation with one eye blinded, either of two simple models could describe the linkage between the eyes. These two alternatives are illustrated in Fig. 48. In both models, the blind right eye is driven by the left seeing eye. In A, the stimulus to the blind eye comes from the input to the seeing eye amplifier, while in B the stimulus to the blind eye comes from the output from the seeing eye amplifier.

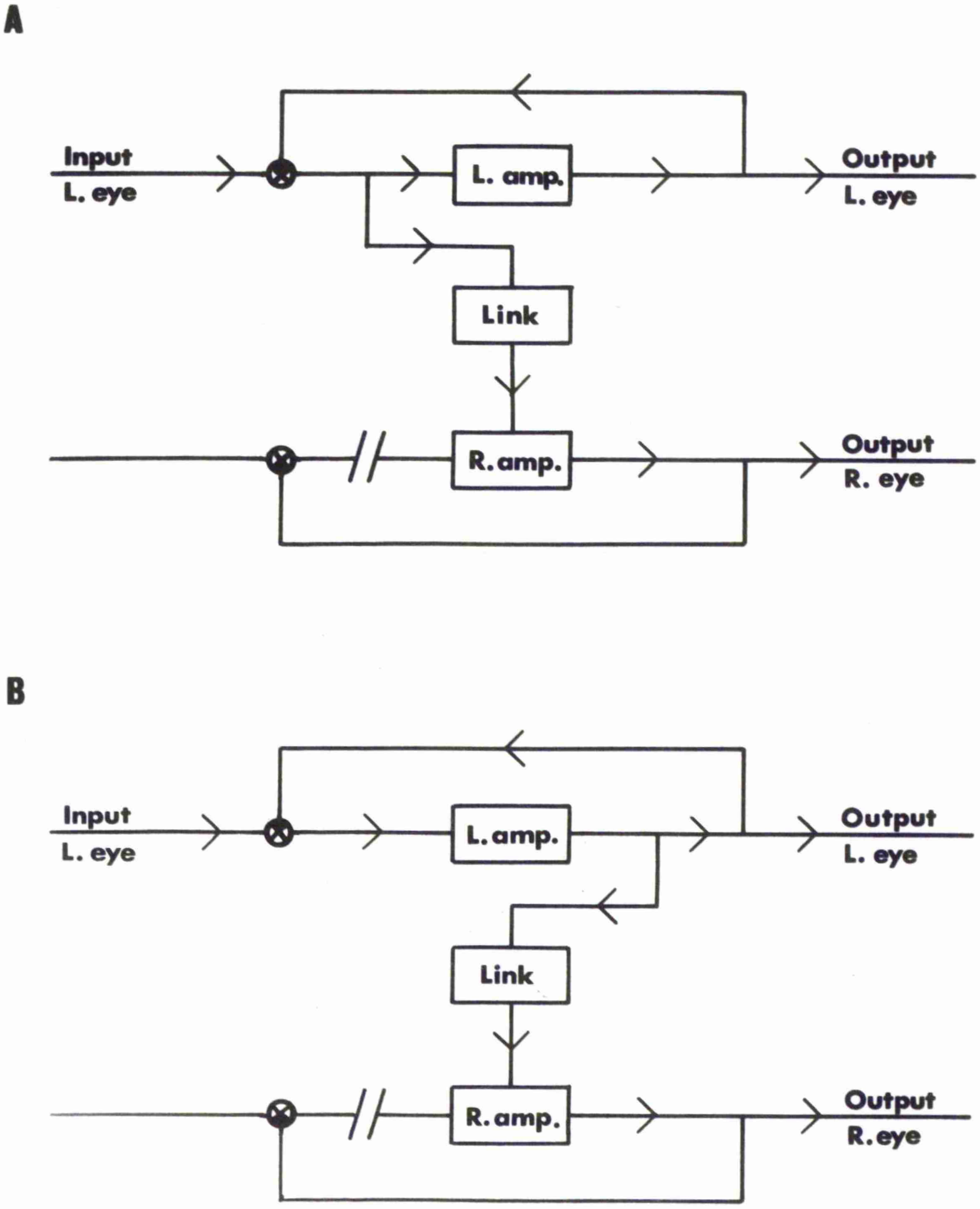
Now if model A holds, then a spontaneous increase in the gain of the left eye amplifier (and variations in gain are common enough) will cause an increase in the left eye output. This output, being fed back and subtracted from the input, will cause the slip speed to be less, and, assuming the gains of the link and right eye amplifiers to be constant, will cause a decrease in the right eye output. To a standard stimulus, there will thus be an inverse relationship between the outputs of the blind and seeing eyes, due to spontaneous changes in the gain of the seeing eye amplifier.

A similar line of reasoning may be applied to model B. Here, a spontaneous increase in the gain of the left eye amplifier will, as above, cause an increase in the left eye output. It will also, however, increase the input to the link amplifier and hence cause an increase in

FIGURE 48.

Two possible models for the linkage between the eyes when one eye is blinded. In both, the blind right eye is driven by the left seeing eye. In A, the stimulus to the blind eye comes from the input to the seeing eye amplifier, while in B the stimulus to the blind eye comes from the output from the seeing eye amplifier.

As is explained in the text, these two models have different properties. If model A holds, then the responses of the two eyes will bear an inverse relationship to each other when one eye is blind; if B holds, the relationship will be a direct one.


A
Input
L. eye
L. amp.
Output
L. eye
Link
R. amp.
Output
R. eye
B
Input
L. eye
L. amp.
Output
L. eye
Link
R. amp.
Output
R. eye

the right eye output. Thus if model B holds, there will be a direct relationship between the outputs of the two eyes.

These relationships will not, of course, be very exact because variations will also occur in the gains of the link and right eye amplifiers. These variations will affect the right eye output alone and hence tend to mask any relationship between the outputs of the two eyes.

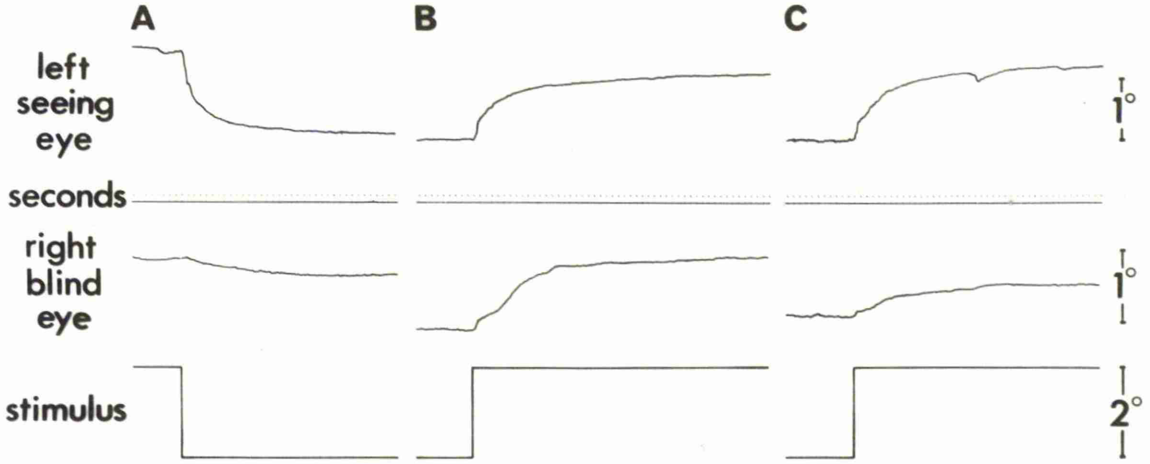
The responses obtained by the left seeing eye and the right blinded eye of one crab to 2° step movements of a striped drum around the animal are illustrated in Fig. 49. In A, B and C the seeing eye responses were, on different occasions, 1.41°, 1.08° and 1.20°. These were accompanied by, respectively, 0.29°, 1.00° and 0.46° blind eye responses. The relationship between the eyes thus appeared to be an inverse one.

Graphs of the seeing eye responses against the blind eye responses to the above standard stimulus were made for five different crabs, and lines of best fit, calculated by the method of least squares, drawn on the graphs. Similar graphs were also made of the responses of the two eyes of the same five crabs when both eyes were free to see and move. This was to determine whether, under normal conditions, there was any correlation between the responses of the two eyes which might mask their relationships when one eye was blinded. Product-moment correlation

FIGURE 49.

Responses of both eyes to 2° step movements of a striped drum. In all traces, the right eye has been blinded.

Note that the relationship between the responses of the two eyes appears to be an inverse one. In A, a 1.41° seeing eye response is accompanied by a 0.29° blind eye one. In B, a 1.08° seeing eye response is accompanied by a 1.00° blind eye response, while in C a 1.20° seeing eye response is accompanied by a 0.46° blind eye response. Movement to the right is shown by a downwards movement of the trace.


A
B
C
left
seeing
eye
seconds
right
blind
eye
stimulus
1°
1°
2°

coefficients were calculated from the data of all these graphs so that the best statistical relationship between the eyes could be established.

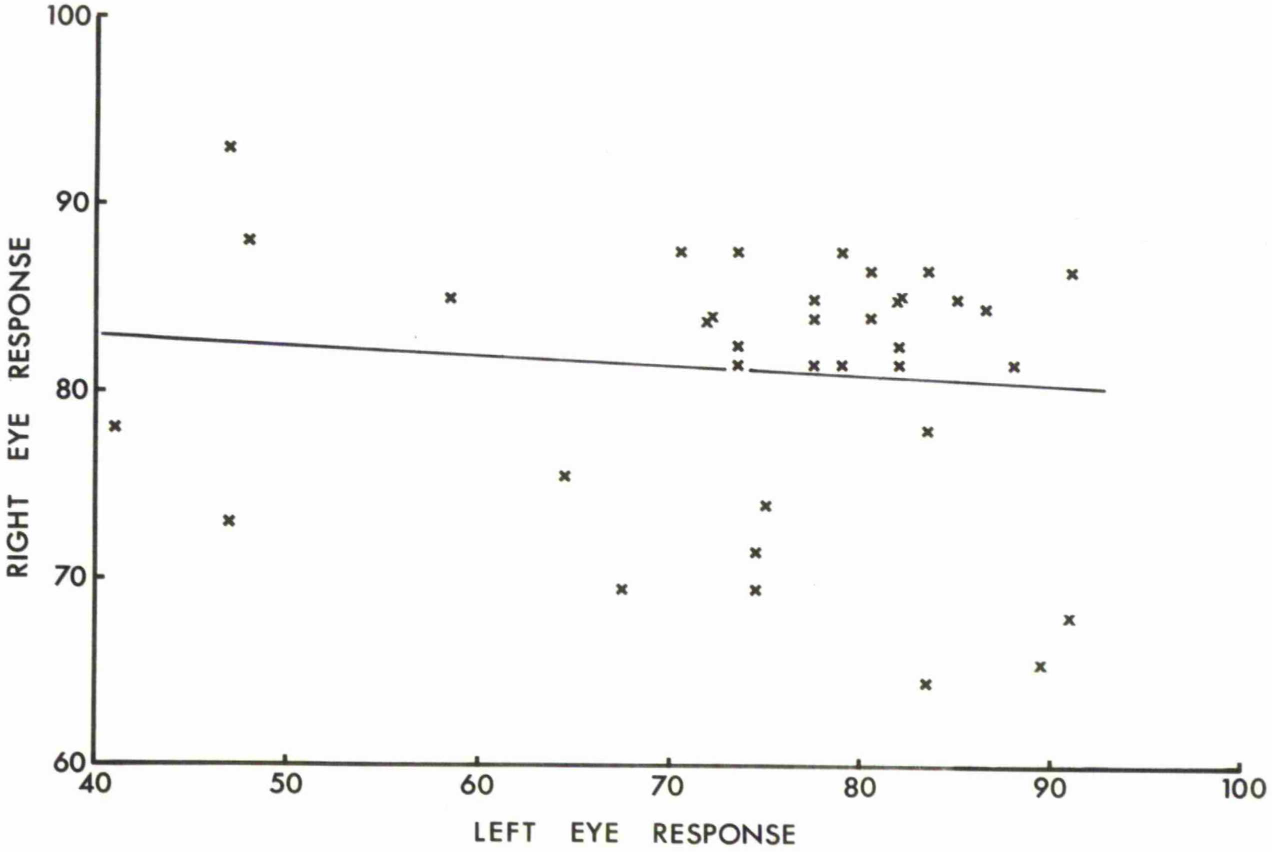
A typical graph of the responses of the two eyes when both were free to see and move is shown in Fig.50. The points are well scattered, the left eye responses having the lower mean amplitude, and showing the greater variation. No correlation could be established between the responses of the two eyes, demonstrating that spontaneous changes in the gains of the left and right eye amplifiers occur independently of each other.

In one of the five graphs however, calculation of the correlation coefficient demonstrated, at the 1% level of significance, that there was a positive correlation between the responses of the two eyes. Further analysis of the data from this crab showed that this direct relationship was due to the amplitude of the responses of both eyes falling off with time. Such a decrease was not unusual in crabs which had been responding for three to four hours, but seldom occurred at the beginning of an experiment. Because of this, the responses of this crab were not further studied.

This left four graphs of blind eye responses against seeing eye responses to be considered. In all four of these, the slope of the line of best fit suggested that there was an inverse relationship between the responses of the two eyes. In two of these graphs, calculation of the product-moment correlation coefficient demonstrated at the 1% level

FIGURE 50.

Graph of left against right eye responses, both expressed as a percentage of the stimulus, to a 2° ramp movement of the striped drum, which can be seen by both eyes of the crab. The line on the graph is the line of best fit calculated by the method of least squares, and illustrates that, under normal conditions, there is no correlation between the responses of the two eyes. All responses were from the same crab.



100
90
80
70
60
RIGHT EYE RESPONSE
40
50
60
70
80
90
100
LEFT EYE RESPONSE

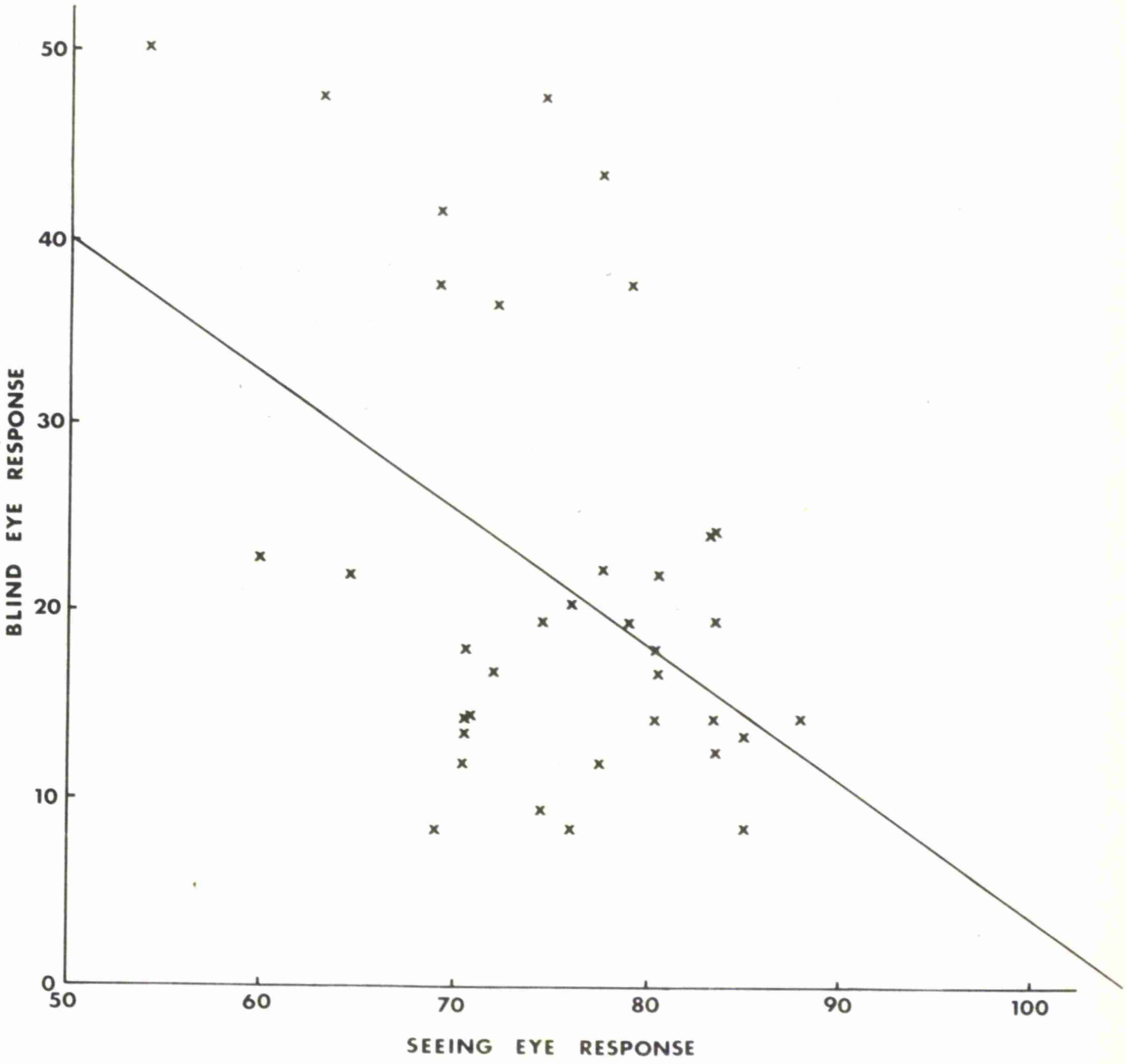
of significance that there was an inverse relationship between the responses of the blind and seeing eyes. One of these graphs is shown in Fig. 51. In the third graph, an inverse relationship was demonstrated at the 2% level. In the fourth, however, no inverse relationship could statistically be established, though the correlation coefficient was negative, suggesting that such an inverse relationship might exist. Thus, though the points on the graphs show considerable scatter, there is an inverse relationship between the responses of the blind and seeing eyes in crabs which continue to respond well, demonstrating that the linkage between the eyes is as in model A and not model B of Fig. 48.

Within each control system amplifier, three different centres have so far been distinguished (see Fig. 28); a <u>movement detector</u> probably in the optic lamina or medulla; a centre called the <u>optomotor centre</u> of unknown location which converts sensory impulses signalling movement into motor impulses to the eye muscles; and thirdly, the <u>eye muscles</u> themselves. Model A may thus be expanded as shown in Fig. 52, the linkage between the eyes being on the movement perception side of the optomotor centre. That Wiersma, Bush and Waterman (1964) have recorded efferent activity from movement receptors in the optic nerve of the crab <u>Podophthalmus</u> suggests that the linkage between the eyes occurs in the optic ganglia.

When one eye is blind, there are no complications as each optomotor centre has only one input. However, when both eyes are seeing, each optomotor centre has two inputs, one from each of the two movement

FIGURE 51.

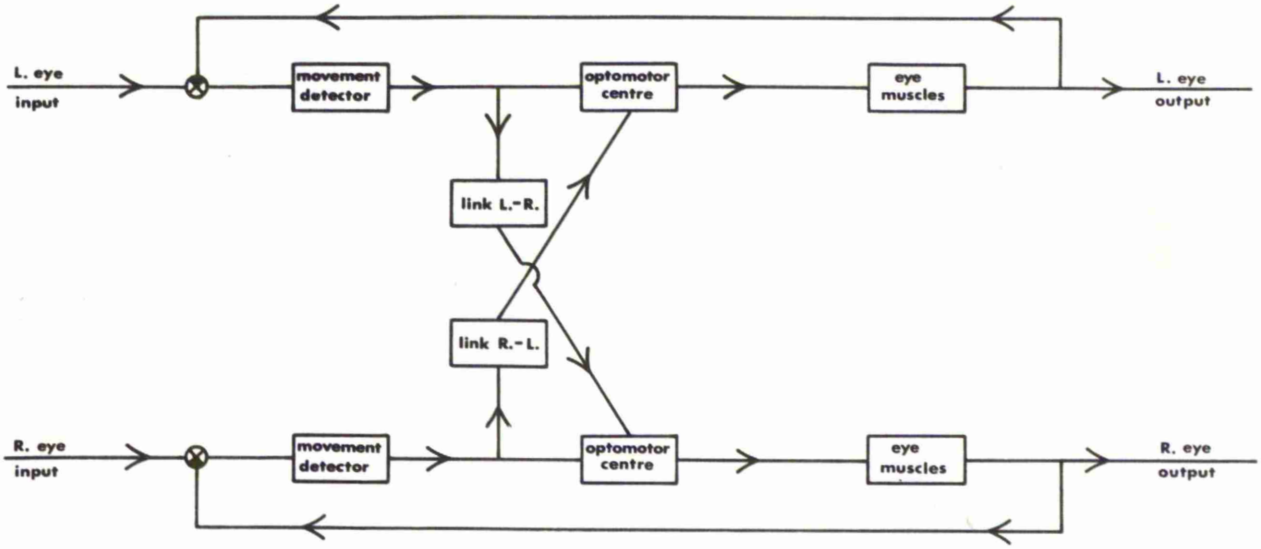
Graph of seeing eye responses against blind eye responses, both expressed as a percentage of the stimulus, to a 2° ramp movement of the striped drum. The line on the graph is the line of best fit calculated by the method of least squares and demonstrates an inverse relationship between the responses of the two eyes when one is blind. All responses were from the crab whose responses are plotted in Fig. 50.



50
40
30
20
10
0
BLIND EYE RESPONSE
50
60
70
80
90
100
SEEING EYE RESPONSE

FIGURE 52.

Block diagram showing the linkage between the two eyes of a crab. For explanation see text.


L. eye
input
movement
detector
optomotor
centre
eye
muscles
L. eye
output
link L.-R.
link R.-L.
R. eye
input
movement
detector
optomotor
centre
eye
muscles
R. eye
output

detectors. These inputs are not simply additive, as a crab with both eyes seeing does not move its eyes twice as far as one with one blind eye. Indeed, when there is any difference at all between the two, and there is none in many crabs, it is an increase in the response amplitude of only 10-20%. Initially, as discussed earlier, the input from the ipsilateral movement detector has most effect, though the input from the contralateral eye may increase or decrease slightly the size of the response. Later on, it is the slower of the two inputs that governs the optomotor centre and hence the responses of the eye, though again the other input may increase or decrease slightly the size of a response, depending upon its direction.

The gains of the link amplifiers cannot be measured directly as they cannot be isolated from the rest of the control system. However, by comparing the response of a seeing eye with the response of the same eye when blinded, the gain of a link amplifier may be approximately determined, for the link amplifier is involved in only the latter of the two situations. In the four crabs whose responses are considered above, calculations of the gain of the L-R link gave the following values:- 0.3, 0.5, 1.2 and 1.3. These values must, however, be viewed with caution, since this method does not account for possible differences in the gains of the two movement detectors. Nevertheless it is reasonable to assume that the link amplifiers are not necessarily of unity gain. There was also some indication that information concerning low velocity stimuli was not transferred across the brain from one eye to another. For instance, the seeing eyes, but not the blinded eyes, of unilaterally blinded crabs responded to drum velocitiew below 0.004°/sec. The low frequency cut off of the link amplifiers may thus be somewhat higher than that of the optomoter centres.

Though this model of the linkage between the eyes is undoubtedly an over-simplification of the existing system, it nevertheless fits all available data, being the simplest system to do so. Such a control system, with loose linkage between the eyes, gives the crab considerable adaptability, and would make possible binocular measurement of distance, though it is not known whether this occurs. It is of interest to note that the situation in man is similar in that the eyes are also loosely linked.

7) INITIATION OF THE FAST PHASE OF OPTOKINETIC NYSTAGMUS.

Almost all the work carried out to date on optokinetic nystagmus has been on the slow phase of the response. The fast phase has hardly received any attention. The following experiments were thus carried out to correct this imbalance and to try to answer the question - what initiates the fast return phase of optokinetic nystagmus?

There are two basically different ways in which the fast phase of nystagmus could be initiated.

The first of these possible mechanisms, proprioceptive feedback, could take several forms. For instance, sensory hairs in the eye socket, of which there are many (Horridge and Sandeman, 1964) could act as position receptors which would signal when the eye had reached the end of its traverse and so cause a fast phase to be initiated. A second form of position reception could occur by means of chordotonal organs similar to those described in limb joints of Crustacea by Bush (1965a,b,c). Such chordotonal organs might occur in the eyestalks and monitor eye position, causing a fast phase to be initiated when the eye reached certain critical positions. A further possibility is that fast phases might be initiated when one or more of the eye muscles reached a critical tension. Myochordotonal organs, which monitor muscle tension, have been described in crustacean limbs by Cohen (1960), and, though neither myochordotonal organs nor chordotonal organs have yet been described in the eyestalks of any crustacean despite a careful search in *Carcinus* by Horridge and Sandeman (1964), the possibility of their existence there cannot be absolutely ruled out.

Should proprioceptive mechanisms be excluded, the second possibility, *central initiation* of fast phases, must be considered. The central mechanism might be relatively independent of the visual input, or alternatively, it might be necessary for the crab to observe movement before fast phases could be initiated. It is unlikely that the *visual input* alone could initiate part phases since there is no fixation by the eye which follows moving stimuli with a constant lag. Central initiation is the general mechanism by which the fast phases of the optokinetic responses of mammals are initiated (Ter Braak, 1936).

As proprioceptive feedback seemed the most obvious way for the fast phase to be initiated, the first experiments were designed to test for possible position receptors.

When an eye was pushed with a fine probe past the point at which the fast phase normally occurred, there was no attempted fast phase by that eye, and no fast phase by the other eye.

Secondly, optokinetic responses were induced as usual by rotation of a striped drum around the crab. A stop was then placed in the path of the eye, to prevent it from attaining the position at which fast phases usually occurred. In spite of this, fast phases still occurred at a high frequency.

These two simple experiments demonstrate that eye position was not involved in fast phase initiation. Muscle tension must therefore be considered.

That muscle tension is not involved in fast phase initiation has been shown by an experiment performed by Horridge and Sandeman (1964), in which they cut the oculomotor nerve to the right eye of a crab. Now, as all motor information to the eye muscles concerning optokinetic stimuli is carried in this nerve (Sandeman, 1964), this eye was necessarily incapable of responding optokinetically. They also sectioned the optic nerve to the other eye, which was therefore blind, but could respond optokinetically. Now, rotation of a striped drum around the crab induced normal optokinetic responses, with both slow and fast phases, from the left eye of the crab. Though there was no possibility of proprioception by the right eye as it remained stationary, the possibility remained that feedback from the blind moving left eye could have initiated the fast phases of the optokinetic responses. This is no longer a possibility if the left eye is removed. Nevertheless, after this was carried out, the normal sequence of motor impulses that bring about the slow and fast phases of the optokinetic response could still be recorded from the oculomotor nerve.

We are thus left with the last possibility - that the fast phase of the optokinetic response is centrally initiated; for all kinds of proprioceptive feedback have been excluded by the above experiments.

In Section 6 of the "Results" it was shown that optokinetic nystagmus could be considered in terms of a block diagram in which each eye has its own control system, the two control systems being linked on the sensory side of the brain (Fig. 52). Within each control system, three different centres were distinguished - a movement detector in the optic lamina or medulla, an optomotor centre of unknown location, and the eye muscles. By the above experiments, the eye muscles have been excluded as factors involved in the initiation of the fast phase. We are thus left with the possibilities that either or both of the movement detectors and/or optomotor centres cause the initiation of the fast phase of nystagmus.

Now close examination of the fast phases from both eyes simultaneously (Fig. 10) demonstrated two new facts. Firstly, both eyes always did a fast phase together; neither eye ever did a fast phase alone. Secondly, as discussed in Section 2 of the "Results", during fast phases to the right, the right eye led the left eye by 30-80 msecs; during fast phases to the left, the left eye led by a similar amount.

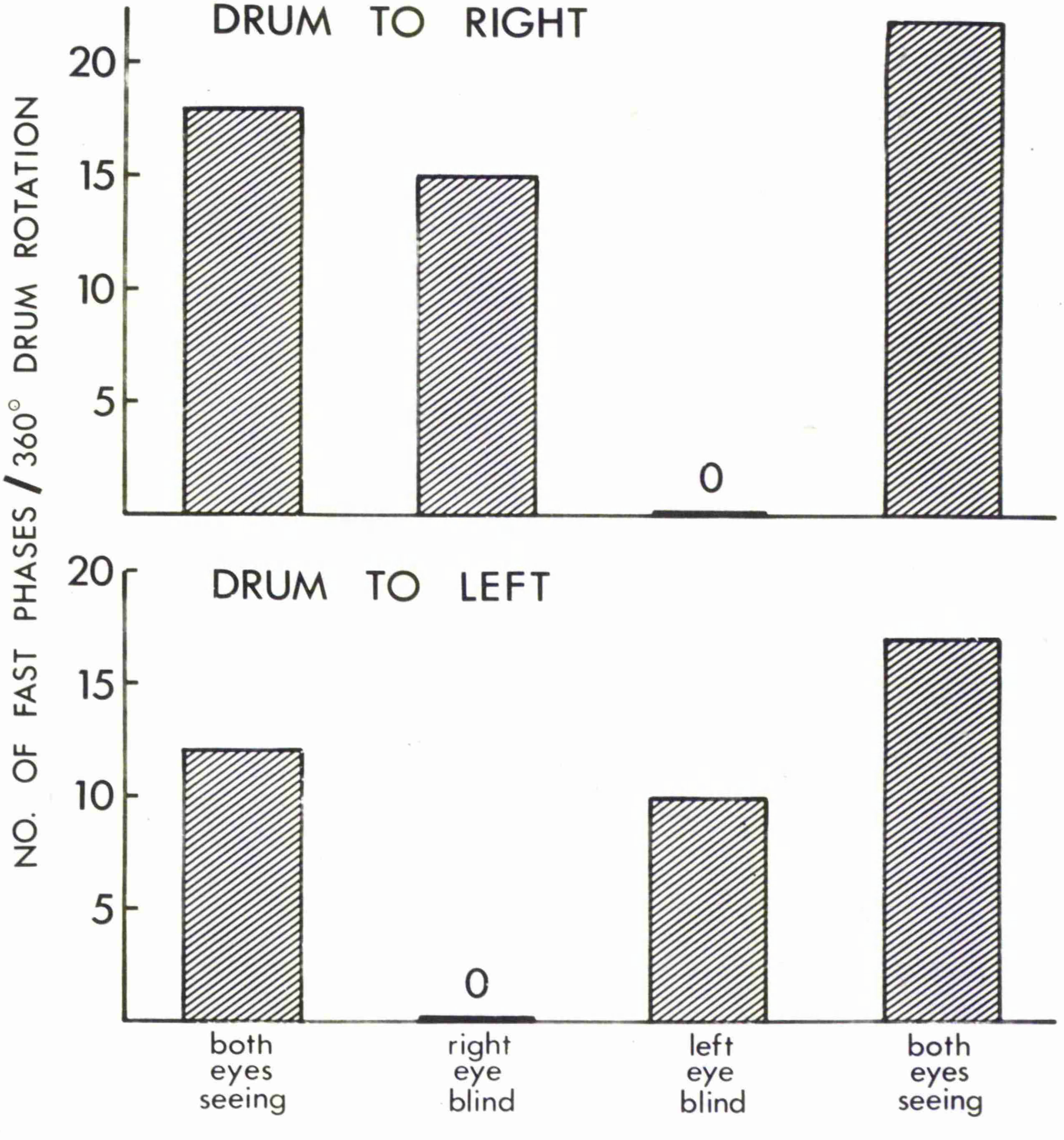
This suggests that the right eye control system initiates fast phases to the right: the left eye control system, fast phases to the left. In fact, this conclusion is readily confirmed by experiment.

The histograms illustrated in Fig. 53 represent the number of fast phases that occurred during the time that the drum was rotated around a crab at a velocity of approximately 5°/sec through 360°. During drum movement to the right, fast phases were, of course, to the left. Here, there were 18 fast phases initially when both eyes could see the drum. Blinding the right eye with black paint reduced this

FIGURE 51.

Histograms of the number of fast phases occurring in response to movement of the striped drum around the crab through 360° at a velocity of approx. 5°/sec. The upper four histograms represent fast phases occurring during movement of the drum in a clockwise direction, the lower four, movement in an anticlockwise direction. After recording the number of fast phases occurring when both eyes could see the drum, the right eye was covered over and the number of fast phases again recorded. Next, fast phases were recorded when the left eye was covered over, the right eye being free to see the stripes. Finally, a second count was made of the number of fast phases occurring when both eyes could again see the drum.

Note that no fast phases to the left occurred when the left eye was blind and no fast phases to the right when the right eye was blind.


DRUM TO RIGHT
DRUM TO LEFT
NO. OF FAST PHASES / 360° DRUM ROTATION
20
15
10
5
0
20
15
10
5
0
both eyes seeing
right eye blind
left eye blind
both eyes seeing

number to 15. This was probably due to a reduction in the velocity of the slow phase, since, as discussed in Section 6 of the "Results", blinding an eye often resulted in a gain reduction of about 10%. When the left eye was blinded, no fast phases occurred; i.e. when the left eye control system had no input, there were no fast phases to the left. When both eyes could again see the drum, 24 fast phases occurred.

Similarly, during drum movement to the left, which produced fast phases to the right, there were no fast phases when the right eye control system had no input.

This experiment has been repeated on more than twenty-five crabs. In most, as in Fig. 54, some fast phases to the right occurred when the right eye was blind, and also some to the left when the left eye was blind. The frequency of such fast phases was, however, always less than one third of the frequency of those occurring in the opposite direction.

We have thus shown that, in order to obtain a normal frequency of fast phases to the left, it is necessary for the left eye to see the stripes, and to obtain a normal frequency of fast phases to the right, necessary for the right eye to see the stripes. Therefore fast phases to the left are initiated by the left eye control system, and fast phases to the right by the right eye control system.

We can however, go further than this, for, as shown in Fig. 55, the main effects of blinding an eye are to cut out the input to the

FIGURE 54.

Record of the slow and fast phases of the optokinetic response of the left eye of a crab to continuous movement of a striped drum around the crab in an anticlockwise direction. Note that when the right eye is prevented from seeing the stripes, few fast phases occur. The arrow indicates 3 small flicks which may have been attempted fast phases. Movement to the right is indicated by a downwards movement of the trace.

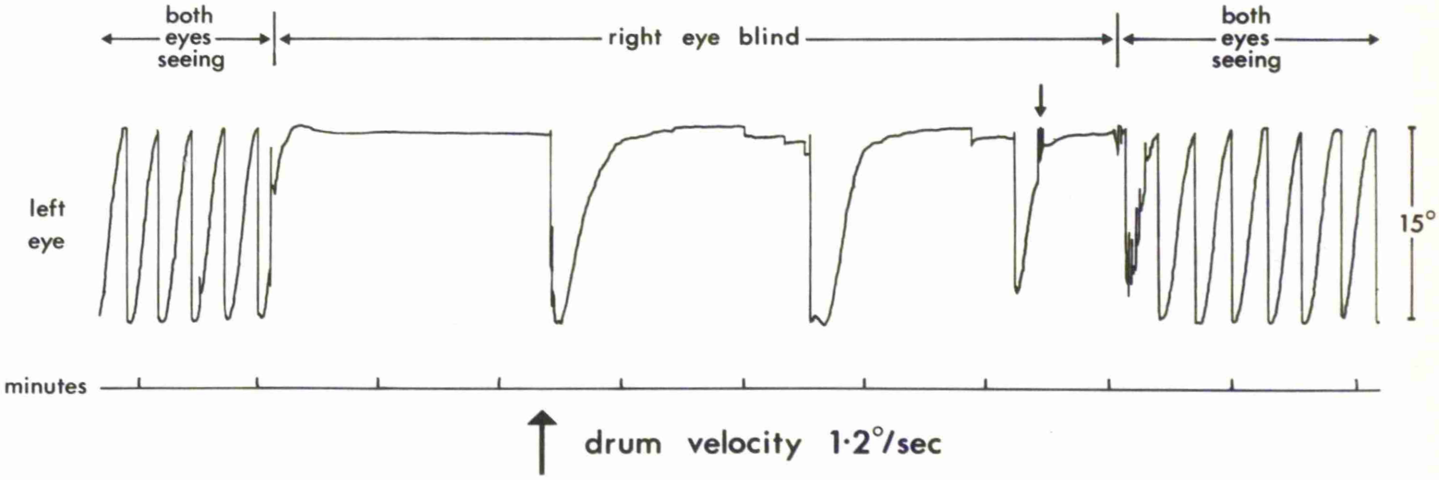
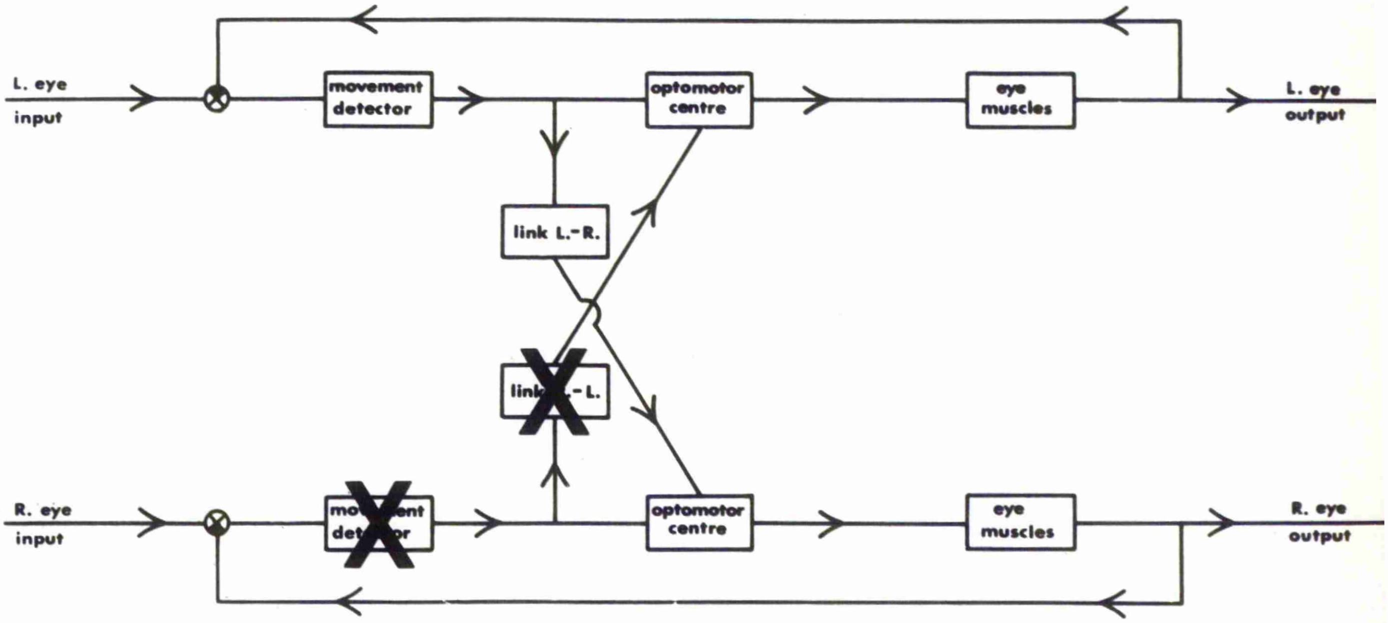

both eyes seeing
right eye blind
both eyes seeing
left eye
15°
minutes
drum velocity 1·2°/sec

FIGURE 55.

The block diagram showing the linkage between the eyes, illustrated in Fig. 51, showing the centres which have no input when the right eye is blinded. These black boxes, marked with a large cross, are the right eye movement detector and the link from the right to the left eye. The rest of the right eye control system gets its input from the left eye via the L-R link.


L. eye
input
movement
detector
optomotor
centre
eye
muscles
L. eye
output
link L.-R.
lin
-L.
R. eye
input
mo
ent
det
or
optomotor
centre
eye
muscles
R. eye
output

movement detector and link on that side. The optomotor centre remains unaffected since it receives an input from the other eye. The link can be reasonably excluded from the argument as it is just an information channel from one eye to another. This means that the movement detectors must be involved in fast phase initiation. However, are the movement detectors the only centres involved?

This question was analysed by recording the movements of both eyes simultaneously and giving each eye a different visual stimulus. In the apparatus used, Fig. 2, the movements of the two sets of stripes could be independently controlled by reversible multispeed motors.

When the eyes saw a different set of stripes, both moving towards the crab's midline at about the same velocity, the eyes squinted, as shown in Fig. 56, but no fast phases ever occurred.

Now if the only centres involved in fast phase initiation had been the movement detectors, fast phases probably would have been initiated. Therefore, the fast phase initiators must also have an input from the optomotor centres of the appropriate control system.

This was confirmed, when, using the same apparatus, both eyes saw movement in the same direction but at different velocities (Fig. 57). In this record, the frequency of fast phases to the left was affected by changes in the velocity of the stimulus to the right eye as well as by changes in the velocity of the stimulus to the left eye.

FIGURE 56.

The responses of the two eyes when each eye saw a different set of stripes. In this record the two loops of stripes were moving in opposite directions, those seen by the left eye to the right and those seen by the right eye to the left. Note that, under these conditions, no fast phases occurred even though both left and right eyes saw movement occurring in the appropriate direction for fast phases to be initiated. Movement to the right is shown by a downwards movement of the trace.

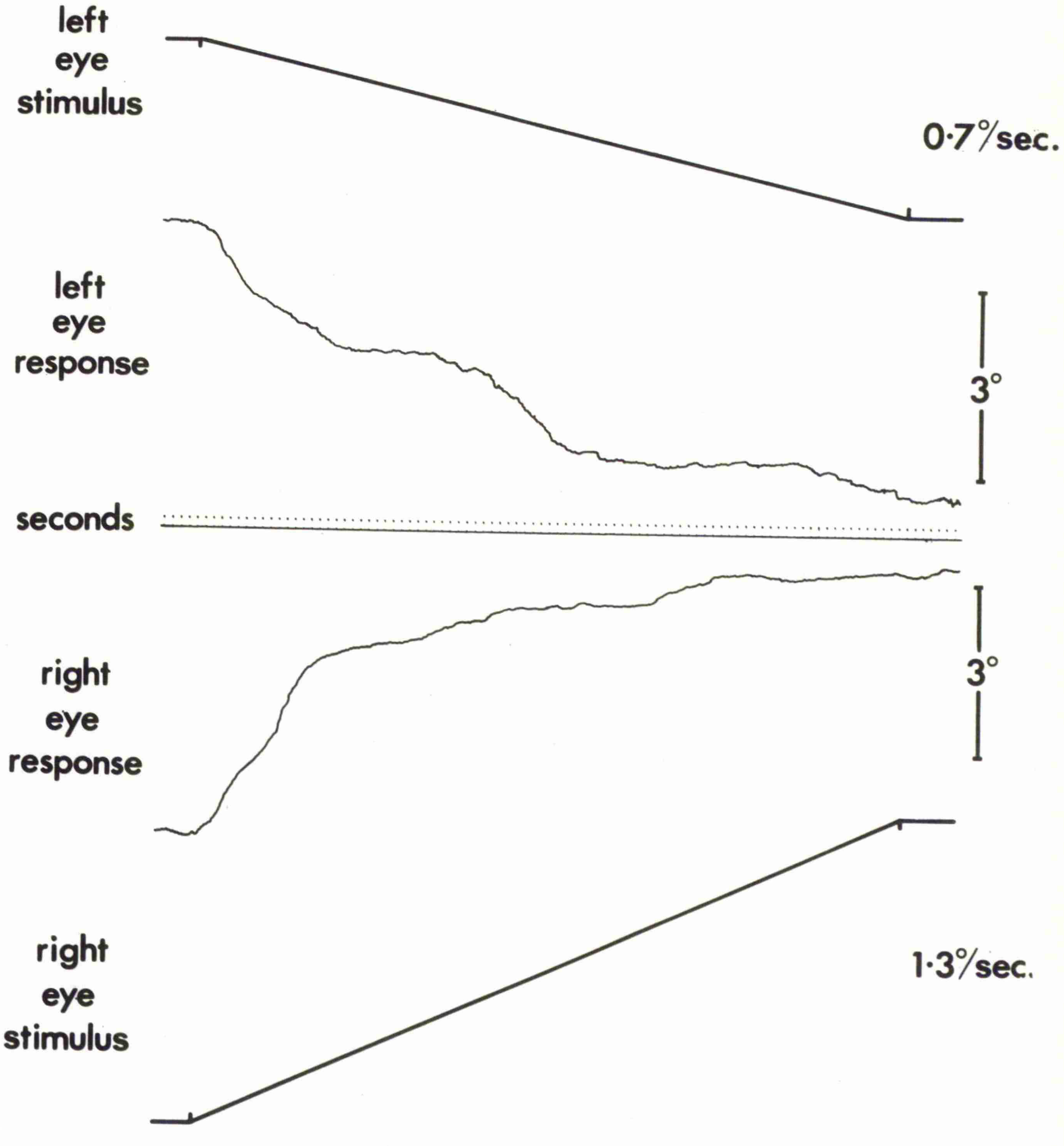
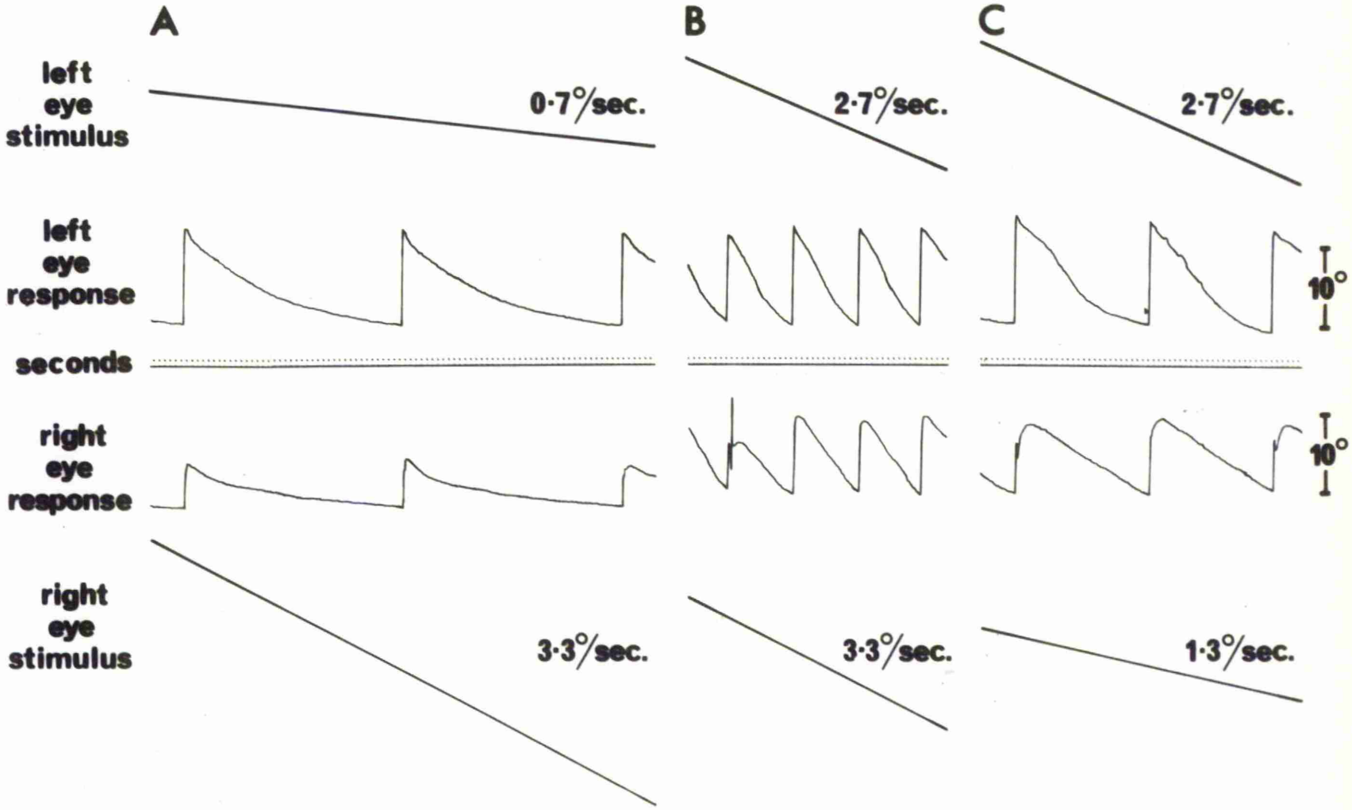

left eye stimulus
0·7°/sec.
left eye response
3°
seconds
right eye response
3°
right eye stimulus
1·3°/sec.

FIGURE 57.

The responses of the two eyes when each eye saw a different set of stripes. In these records, the two loops of stripes were moving in the same direction at different velocities. If A and B are compared, it can be seen that a change in the velocity of the stimulus to the left eye, the right eye stimulus velocity remaining constant, results in a change in the frequency of fast phases. Similarly, a comparison of B and C shows that a change in the velocity of the stimulus to the right eye (left eye stimulus velocity constant) also results in a change in the fast phase frequency. Movement to the right is shown by a downwards movement of the trace.

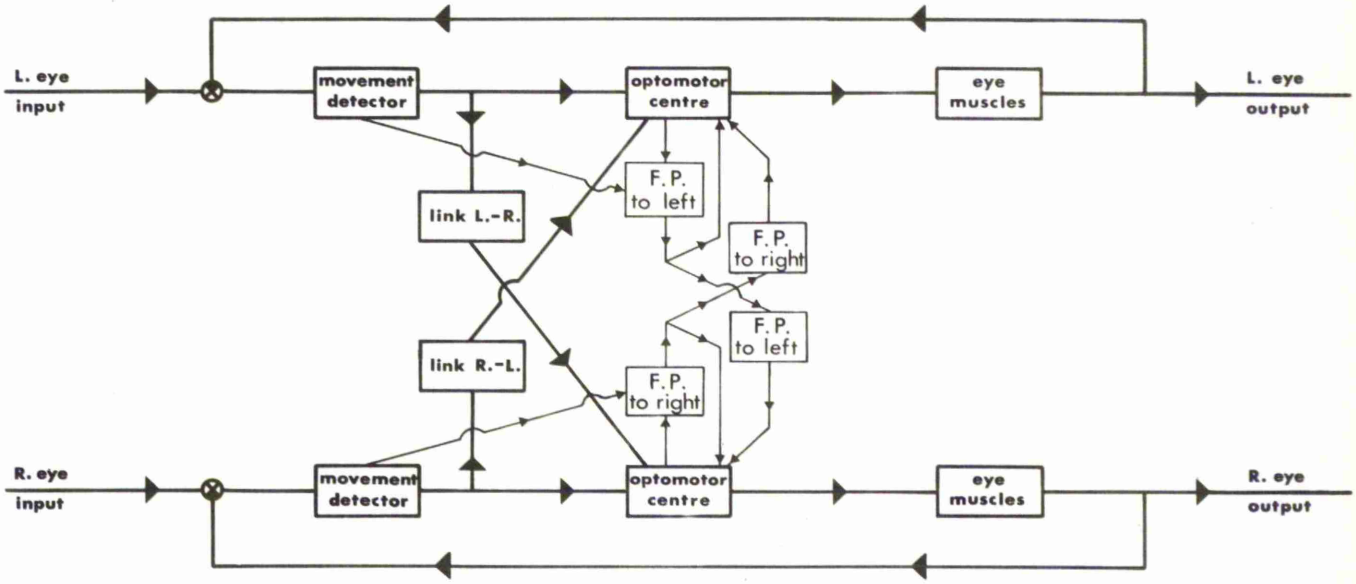
A
B
C
left eye stimulus
0·7°/sec.
2·7°/sec.
2·7°/sec.
left eye response
10°
seconds
right eye response
10°
right eye stimulus
3·3°/sec.
3·3°/sec.
1·3°/sec.

This was shown graphically in Fig. 43. On this graph, the mean interval between successive fast phases are plotted against the velocity of the stimulus to the right eye. It shows that, with the stimulus to the left eye remaining constant, increasing the right eye stimulus velocity caused a decrease in the interval between fast phases. Similarly, an increase in the left eye stimulus velocity from 0.75°/sec to 3.0°/sec caused a decrease in the interval between fast phases. If the left eye movement detector had been the only centre involved, changes in the velocity of the stimulus to the right eye should not have affected the interval between fast phases. Only changes in the left eye stimulus velocity should have had any effect. The optomotor centres as well as the movement detectors must therefore be involved in fast phase initiation.

The block diagram, Fig.58, is thus the final model that has been deduced by the above experiments. The fast phase initiators, which may be single neurons or groups of neurons, receive inputs from both the movement detectors and the optomotor centres of the appropriate control system; i.e. initiators of fast phases to the left from the left eye control system, those of fast phases to the right from the right eye control system. Since the fast phases of the two eyes do not occur simultaneously, one eye always leads the other by 30-80 msecs, paired centres are proposed rather than single ones. It is suggested that one of each pair always fires off the other, and that this causes the 30-80 msecs delay.

FIGURE 58.

The control system for both slow and fast phases of optokinetic nystagmus. For explanation see text.



L. eye input
movement detector
optomotor centre
eye muscles
L. eye output
F.P. to left
link L.-R.
F.P. to right
F.P. to left
link R.-L.
F.P. to right
R. eye input
movement detector
optomotor centre
eye muscles
R. eye output

It has also been noted that actual movement must be seen by the crab for fast phases to occur at their normal frequency. Memory and step stimuli, which cause large responses in the slow phase of the optokinetic response, usually failed to initiate more than an occasional fast phase. However, when the eye was near the end of its traverse, fast phases could often be initiated by, for instance, touching the carapace. The importance of the visual input in fast phase initiation thus remains unclear.

It can, however, be said in conclusion, that for the normal fast frequency to the left to occur, the crab must be observing actual movement towards the right with its left eye. Only under these conditions are fast phases initiated at anything like their normal frequency by the optomotor centre of the left eye control system. But, of course, the actual trigger in terms of the neurons involved is still unknown. A possibility is that it is a critical impulse frequency in the neurons that go from the optomotor centre to the eye muscles. However, there are many of these, all with different impulse frequencies; also they are of two types, tonic and phasic; and worst of all, all units studied so far reach a constant impulse frequency several seconds before the fast phase occurs (Burrows, personal communication). Therefore these efferent neurons do not appear to be good candidates for the job of fast phase initiation.

The final problem thus remains unsolved, for the actual trigger to the fast phase initiators remains undiscovered; and its discovery would only complete the model, obviously a great over-simplification of the existing system.

DISCUSSION

Since many of the theoretical implications of the experiments described in this thesis have already been analysed, this discussion will necessarily be of a general nature. It is primarily an attempt to build up a picture of the optokinetic reflex as a whole from experimental results which were each individually concerned with only a small part of the response, and to relate these conclusions both to wider aspects of vision and to the movements and optokinetic responses of the eyes of mammals. Consideration will also be given to the function of these eye movements in the normal life of the crab, for it is difficult to imagine a complex reflex such as the optokinetic response being evolved and yet conferring no biological advantage on the animals that possess it.

ANALYSIS OF A REFLEX

The control system governing the optokinetic responses of the eyecups of Carcinus incorporates a negative visual feedback loop, since the movements of the eyecups in following the visual field reduces the apparent velocity of that field. Although units have been found in the optic nerves of several decapods conveying mechanoreceptive and proprioceptive information from the eye apparatus (Waterman and Wiersma, 1963; Bush, Wiersma and Waterman, 1964), and similar fibres are presumed to exist in *Carcinus*, all experiments lead to the conclusion that this information is not utilised in the formation of a proprioceptive feedback loop. The control of eye movements by visual feedback alone is thus in direct contrast to the movements of the walking legs of *Carcinus*, which have been shown by Bush (1962) to be controlled by proprioceptive feedback. It may even be that *Carcinus* cannot distinguish between apparent movement induced by itself and real movement of the environment, for there is little evidence for any system, such as the "reafference" system proposed by von Holst and Mittelstaedt (1950), that anticipates and neutralises the visual change that occurs when the animal initiates its own movement.

The control system for optokinetic responses appears in its simplest form in Fig. 8B, though subsequent experiments have shown that the system is considerably more complex than this. Firstly, the occurrence of optokinetic memory responses necessitates the incorporation of a memory store into the block diagram. A position feedback loop should also be included, however, for the presumed stimulus in the memory situation (the mismatch between the present and remembered positions of the stripes) is progressively reduced as the response occurs. Secondly, experiments in which the responses of both eyes were recorded simultaneously have shown that each eye has its own system for converting perceived motion into eye movement. These systems interact with each other, for when the two eyes have conflicting visual inputs, their responses are only partially independent of each other. Finally, additional centres must be inserted to account for the initiation of the fast phase of optokinetic nystagmus. Although all these degrees of complexity have not been represented on any one diagram, the complete control system for all optokinetic responses described so far could be obtained by a combination of Figs. 28 and 58. It must be stressed, however, that these diagrams are only models and, though representative of our knowledge of the control system to date, are certainly a gross oversimplification of the existing system.

On the input side, a motion perception system such as that proposed by Hassenstein and Reichardt for the beetle Chlorophanus (Hassenstein and Reichardt, 1956; Hassenstein, 1958a,b; Reichardt, 1957, 1961, 1962), could be responsible for all responses except those attributable to the memory system. Although no experiments were designed to test this model, the amplitude of the eye responses to the apparent movement of pinlights were only proportional to the stimulus for stimulus amplitudes of up to 3 - 4°. This suggests that movement correlation only occurs between adjacent or subadjacent ommatidia, in agreement with Hassenstein and Reichardt's model.

That memory responses are not attributable to the same system is indicated by the experiments in which open and closed loop memory responses were compared, for these experiments showed that memory responses can only be described by a system which incorporates position as well as velocity components. Indeed, Horridge (1966f) has shown that the two systems are quite separate from each other, for when the eyecup response of Carcinus to a low amplitude, 3 c.p.s., oscillatory stimulus was almost fully adapted, the memory component of the response to a subsequent step stimulus was still obtained, even though the velocity component was absent.

Of the numerous afferent fibre types identified in the optic tracts of decapods by Waterman and Wiersma (1963), Waterman, Wiersma and Bush (1964), Wiersma and Yamaguchi (1966) and Wiersma (1967), only the unidirectional movement fibres seem relevant to the optokinetic responses. Indeed, it is likely that they form the afferent pathway of the reflex. Although no fibres have been found that respond to movements below 0.01°/sec or to memory stimuli, the absence of such units is in no way significant since no experiments have yet been carried out that would reveal the existence of such fibres (Wiersma, personal communication).

These movement fibres form the input to a pair of centres, the optomotor centres, which are probably located in the protocerebrum and are responsible for generating the motor impulses that drive the eye muscles. These centres are thought to be the main amplifiers of the eye movement control system since their input depends upon the stimulus and their output is reflected in eyecup movement. The gain of these amplifiers depends not only upon stimulus velocity, being highest when this is approximately 0.01°/sec, but also upon the number of movement fibres stimulated. For instance, movement of a pinlight, which causes excitation in only a few movement fibres, induces a response of lower gain than movement of a multi-striped drum at the same velocity. A similar summation of the outputs of all the movement fibres must occur in *Chlorophanus* (Reichardt, 1962), for when the upper and lower halves of the eyes of this beetle see stripes moving at identical velocities but in opposite directions, the optomotor turning tendency is zero. Changes in the gain of these amplifiers also arise internally, for consecutive open loop responses to repeated stimuli show considerable variation (Fig. 32B). During closed loop responses, this scatter is considerably reduced (Fig. 32A), for negative feedback loops have the property of reducing response variability. In particular, considerable increases in gain accompany leg waving and eye scanning.

The other main non-linearity of the optokinetic response, the considerable adaptation of the responses to stimuli in the velocity range 2 - 20°/sec, probably occurs at the input to the movement fibres, since, in the crab *Podophthalmus*, units responding to this velocity range show considerable adaptation (Waterman, Wiersma and Bush, 1964).

Experiments in which the responses of both eyes were recorded simultaneously show that each optomotor centre receives an input from both eyes. During the first few seconds of an optokinetic response in which the two eyes have conflicting visual inputs, the outputs of the optomotor centres are largely governed by the inputs from the movement fibres of the ipsilateral eyes. After a few degrees of movement, however, both eyes either come to a standstill, or move in the same direction, usually at similar velocities. Thus, both optomotor centres are, in the end, dominated by the movement fibres from only one of the eyes.

The motor output programme to the eyecup muscles during optokinetic responses is determined by the ipsilateral optomotor centre with no reference to whether the eye moves or not, or even whether it is still attached (Horridge and Sandeman, 1964). The complexity of this programme is considerable, for, of the nine muscles in each eyecup, eight are involved in optokinetic responses, and each of these is innervated by both a fast and a slow axon from the oculomotor nerve (Burrows, 1967a). The movements of the eyecups are also very varied, for they will follow vertical as well as horizontal movements of contrasting stimuli, and will even follow the movement of a pinlight in a circle in an otherwise dark visual field. Burrows (1967a) has further shown that the motor output programme is different, not merely reversed, during optokinetic responses in different directions in the horizontal plane. These horizontal responses are further complicated by the periodic intervention of fast phases of nystagmus.

The onset of the fast phase of nystagmus cannot be determined by the position reached by the eyecup, for fast phases occurred at a high frequency when the eyecup was prevented by a stop from reaching the position at which fast phases were usually initiated. Similarly, tension receptors in the muscles are not involved, for the central programme of impulses which determines both slow and fast phases of nystagmus could be recorded even when the eyecups were prevented from moving by section of both oculomotor nerves (Horridge and Sandeman, 1964). It was thus concluded that fast phases must be centrally initiated or depend in some way upon the visual input.

Two experiments indicate that fast phases to the left are initiated by the left eye control system, those to the right by the right eye control system. First, during fast phases to the right, the right eye always led the left eye by 30 - 80 msec; during fast phases to the left, the left eye led by a similar amount. Second, when the right eye was prevented from seeing the striped pattern, very few fast phases occurred to the right. Similarly, when the left eye was blind, few fast phases occurred to the left.

Since each optomotor centre received an input from both movement detectors (Fig. 52), the second of these experiments indicates that the movement detectors must be involved in fast phase initiation. However, the optomotor centres must be involved as well, for the frequency of fast phases could be influenced by changing the input to either eye (Fig. 57).

The control system (Fig. 58) thus incorporates fast phase initiators, which may be single neurones or groups of neurones, which receive inputs from both the movement detector and the optomotor centre of the appropriate control system. The fast phase initiators act on the appropriate optomotor centre, changing the motor output programme so that a fast phase of nystagmus occurs. Though the influence of the movement detectors is obscure, since some fast phases occurred in both directions when one eye was blinded, it appears that fast phases are initiated at their normal frequency by the appropriate optomotor centre only when the crab is observing actual movement towards its midline. It is possible that the actual trigger is a critical impulse frequency in one of the neurones that go from the optomotor centre to the eye muscles. However, there is no experimental evidence for this, and the large number of candidates involved makes this hypothesis difficult to test.

FUNCTION OF EYE MOVEMENTS

Since several observations suggest that eye tremor is, to some extent at least, under central control, it is reasonable to expect it to have a function in vision. Indeed, experiments performed by Horridge (1966b) and described in the 'Introduction' indicate that eye tremor accentuates the perception of the edges relative to the areas of a vertically black and white striped drum. Presumably the tremor has the effect of preventing the adaptation of those receptors which face the edges of the striped pattern, while receptors which continuously face either a black or a white area would be expected, from properties of receptors in general, to adapt towards a background frequency.

It may also be that eye tremor aids the perception of stationary objects by the crab, for Horridge and Sandeman (1964) showed that a clamped eye, facing a stationary contrasting pattern, was much less effective in inhibiting the optokinetic response of the other eye to a moving pattern than the same eye when free to move.

The function of saccades, drift and eye scanning is much harder to assess, and no experiments have been performed which suggest any visual role for these movements. It may be that eye scanning is related to the movements of the eyes during walking, since it is always associated with leg movements. If, on the other hand, it is related to the eye scanning of *Pachygrapsus* which occurs when a strange object is introduced into the visual field (Sandeman, personal communication), then it may, like tremor, serve to sharpen up contrasts in the visual field.

In the same way, the significance of the optokinetic responses lies not in the movements themselves but in their effect in modifying the visual input to the eye, for, during its normal life in the intertidal zone, *Carcinus* probably never executes a complete optokinetic response with both slow and fast phases of nystagmus.

If, as suggested above, *Carcinus* is unable to distinguish between real movement and apparent movement induced by its own turning, then the possession of a mechanism whereby the eyes could be as far as possible stabilized on objects in the visual field would be useful for it would minimize the confusion that arises from this situation. That the optokinetic responses provide such visual stabilization is indicated by several observations. In particular, the eye drift that occurred whenever there were no contrasts in the visual field was considerably reduced when the crab viewed a stationary striped drum or even a single stationary pinlight. Indeed, all closed loop following optokinetic responses cause a considerable reduction in the velocity of the 'retinal image' of objects in the visual field.

During optokinetic responses to low velocity stimuli, the visual input must be averaged over several seconds before movement can be deduced. Optokinetic memory is thus a system whereby small irregularities in the eye movement can be smoothed, as well as a system enabling very slow movements to be stabilised. Eye flicks and partial retractions are also stabilized by the memory system, for the eye usually returns to its original position following these movements (Horridge, 1967a).

That the highest gain optokinetic responses occur in response to stimuli moving at approximately the speed of the sun across the sky (Horridge and Sandeman, 1964), and that the eyes do indeed follow the movement of the sun in the absence of stationary contrasts in the visual field (Horridge, 1966e), seems relevant to the use of the sun or moon in navigation or orientation. Though, as described earlier, there is little evidence for any navigational ability in <u>Carcinus</u>, several other crustaceans, notably the amphipods <u>Talitrus</u> and <u>Talorchestia</u> studied by Pardi and Papi (1961), are known to use the sun as a compass and there is no reason to believe that Carcinus cannot do likewise. Certainly Carcinus can measure the angle of movement and velocity of the sun with sufficient accuracy for an onshore or seaward migration (as indicated by its optokinetic responses to the movements of pinlights at different angles to the horizontal), even if not for more complex navigation involving computation of latitude and longitude.

COMPARISONS WITH MAN AND OTHER MAMMALS

Normal eye movements

The tremor, drift and flicks of the eyes of crabs may conveniently be compared to similar movements that occur in mammals. In man these movements have been extensively studied for over fifty years by photographic techniques and, more recently, by a variety of reflection methods. The most widely used of these is that of Ditchburn and Fender (1955), who recorded the movements of a beam of light which was reflected from a mirror carried on a stalk on a contact lens.

Eye tremor in man is composed of irregular oscillations with a frequency spectrum of up to 150 c.p.s. (Fender, 1956), but with most of the power at frequencies below 50 c.p.s. Its median peak to peak amplitude is about 0.005°. There are two main hypotheses concerning its function in vision. One school holds that the minute movements of the image on the retina, caused by the eye tremor, enhances vision by sharpening acuity and contrast. Others believe that the only function of these eye movements is to counteract adaptation by constantly shifting the image across the receptors.

These hypotheses have been investigated by the use of stabilized image techniques in which stimuli are presented which move exactly in step with the tremor of the eye. Under these conditions, stimuli appear to fade with prolonged inspection, but Keesey (1960) found that acuity is initially no worse than under normal viewing conditions. Fender and Nye (1962), on the other hand, found that the accuracy with which a pair of lines positioned end to end could be aligned was, under certain conditions, reduced during stabilized vision. Also, stabilized images frequently reappear after fading (Evans and Piggins, 1963) and this reappearance is not wholly due to contact lens slip, as supposed by Barlow (1963), for reappearances as well as disappearances are sometimes partial and are far from being random. Furthermore, when patterned targets are viewed as prolonged afterimages (Bennett-Clark and Evans, 1963) which obviates the use of contact lenses while maintaining the target stationary on the retina (Craik, 1940), the target still reappears after fading. Thus the second hypothesis, which predicts permanent disappearance of stabilized images, certainly oversimplifies the function of tremor, though the evidence for the first hypothesis remains inconclusive. Although the exact function of tremor is thus obscure, it seems that, in spite of the dissimilarity between simple and compound eyes, and the marked differences in tremor amplitude and frequency, tremor plays a similar role in vision in both men and crabs.

The drift and saccades of the eyes of Carcinus and man are not so comparable, however, for in crabs these movements are, respectively, irregular and infrequent when the animal faces a contrasting visual field, while in man they alternate continuously even during fixation.

In man, eye drift of median velocity 0.07°/sec is interrupted at intervals varying from 30 msec to 5 secs by saccadic flicks of approximate duration 25 msec and amplitude 0.015 - 0.3° (Ditchburn and Ginsborg, 1953). From his recordings of eye movements during fixation, Boyce (1967) shows that the elliptical overall fixation area, the fovea, is subdivided into a series of overlapping short-period fixation areas, upon which the image is fixated for periods of up to a few seconds. Saccades occurring during fixation have one of two functions. They either return the image to the short-period fixation area (compensation for drift) or else shift the image from one short-period fixation area to another, possibly to avoid fatigue of the retinal receptors. The saccades of the eyes of Carcinus cannot have such functions, however, for the eyes do not fixate, most if not all of the ommatidia being equivalent to each other.

The eye movement control system

The control system for the optokinetic responses of Carcinus, illustrated in Fig. 28, incorporates both velocity and position visual feedback loops and comparable feedback loops are present in the control system for directing human gaze at a moving target.

The positional feedback generated in man during such a tracking task is due to an error signal which is induced when the image is displaced from the fovea (Fender and Nye, 1961). Such an error signal is usually corrected by saccadic eye movements, which are essentially ballistic in that the decision concerning their direction and magnitude is taken before movement begins, the saccades then following an inevitable course (Westheimer, 1954). Since the ability to extract such an error signal is only present in a very limited region of the retina (Fender, 1964), it differs from the mismatch signals which initiate optokinetic memory responses in _Carcinus_, for the latter do not depend upon particular ommatidia being stimulated. The responses to these signals are also different, for the memory responses of _Carcinus_ are smooth movements during which the eyes see normally (Horridge, 1966g), while vision is centrally suppressed during the saccadic correcting eye movements of man (Zuber and Stark, 1966).

That retinal image motion also generates velocity feedback in man has been demonstrated by Fender (1964), who suddenly displaced and then slowly returned a stabilized target to the visual axis. The initial displacement initiated a series of saccades, a fruitless attempt by the eye to return the image to the fovea. The slow return of the target, on the other hand, initiated a smooth movement of the eye in the same direction as the target motion, even though this was in the opposite direction to the displacement of the target from the fovea. The response was thus initiated by the movement of the target and not by its displacement from the fovea. Such velocity signals always generate smooth pursuit movements, and, like the movement fibres identified in decapods by Waterman and Wiersma (1963), are thought to be the signals involved in optokinetic nystagmus.

Although the evidence is by no means conclusive (c.f. Section 2 of "Results"), it seems probable that Carcinus cannot distinguish between apparent movement induced by its own eye movement and actual movement of the environment. Certainly, information from proprioceptors in and around the eyestalk is not used in the control of eye movements, but although there is no evidence for an oculomotor feedback pathway, the possibility that such a pathway exists cannot be altogether excluded.

The theory that man distinguishes between world motion and self motion by monitoring and feeding back the oculomotor output to the eye muscles to some more central level was first put forward by Helmholtz in 1867 (Helmholtz, 1962). This theory has withstood many objections (e.g. Sherrington, 1918), and has recently received experimental support from Brindley and Merton (1960) who have confirmed that the eye has no position sense. The function of the muscle spindles in the extrinsic eye muscles thus remains an enigma. Fender and Nye (1961) suggested that the phasic output of these muscle spindles, demonstrated by Cooper, Daniel and Whitteridge (1955), was used in the formation of a negative velocity feedback loop for the control of eye movement. In a revised block diagram, however, Fender (1964) excludes this proprioceptive feedback loop but does not suggest any other function for these muscle spindles. It may thus be that the eyes of Carcinus and man are similar in having no position sense but differ in their ability to distinguish self motion from world motion.

Optokinetic responses

Most mammals exhibit optokinetic nystagmus when a vertically black and white striped cylinder is rotated around them. Like the equivalent responses of the crab, mammalian optokinetic nystagmus is composed of two phases, a slow phase during which the eyes move in the same direction as the stripes, and a fast return phase in which the eyes are flicked back in the opposite direction. In both mammals and crabs, unidirectional movement units are thought to form the afferent pathway of the response, and the oculomotor outputs to the eye muscles are also comparable, for in the cat, as in Carcinus, the efferent impulse frequency to the muscles causing the slow phase movement increases as the slow phase of nystagmus progresses (McIntyre, 1939). These neurones are silent during the fast phase of the response, when there is a burst of impulses in the neurons innervating the antagonistic muscles.

The lower limit of the optokinetic response of both dogs and rabbits (Ter Braak, 1936; Rademaker and Ter Braak, 1948) is similar to that of Carcinus, eye movements being obtained in response to a stimulus velocity of 0.0017°/sec, equivalent to 360° of rotation in 60 hours. This is a much lower velocity than can be appreciated by man. At the other end of the scale the optokinetic response of the rabbit, like that of Carcinus, fails at drum velocities in the range 20 - 70°/sec. Dogs and monkeys, on the other hand, will respond to stimulus velocities of more than 360°/sec.

Except at the extreme limits of the response, the gain of the slow phase of mammalian optokinetic nystagmus is high, the eyes moving almost as fast as the stripes in the closed loop condition, and at sixteen times the velocity of the stripes when all visual feedback is abolished by blinding one eye and fixing the other. Even when the optokinetic response is induced by the movement of a single light source in the absence of stationary contrasting objects in the visual field (Ter Braak, 1936; Rademaker and Ter Braak, 1948), the gain of the response is only slightly reduced and fast phases are readily obtained. Although the intensity of the light source used in these experiments is not stated, and may well be much greater than that of the pinlights used to stimulate Carcinus, it is clear that under most conditions the gain of mammalian optokinetic nystagmus is higher than that of Carcinus.

Rademaker and Ter Braak (1948) have also shown that rabbits exhibit after-nystagmus, for when stimulation by the rotating cylinder is abruptly checked by switching off the light, the optokinetic response does not stop at once, but continues for several seconds. In the dog, which, unlike Carcinus, also shows this response, an optic after-nystagmus of more than 40 slow and fast phases has been observed.

During monocular optokinetic stimulation of Carcinus, few fast phases of nystagmus occurred unless the stripes were moving from the lateral to the medial edge of the eye, for fast phases to the right are initiated by the right eye control system, those to the left by the left eye control system. Comparable inequalities in the contributions of the two eyes to the optokinetic response have been observed in rabbits. This asymmetry is revealed by two types of experiment. Firstly, during monocular stimulation, the gain of the optokinetic response is considerably greater when the pattern moves from the temporal to the nasal edge of the eye than when it moves in the opposite direction (Ter Braak, 1936; Fukuda and Tokita, 1957). Thus, during binocular optokinetic stimulation, one eye contributes more to the response than the other. Secondly, when central nystagmus, elicited by electrical stimulation of an optic tract, is combined with synergistic optokinetic stimulation of one eye only, the central nystagmus is enhanced. This potentiation is greatest when the eye that views the stripes is the one that, under binocular stimulation, contributes most to the optokinetic response (Bergmann et al, 1963).

The fast phase of nystagmus of mammals, like that of <u>Carcinus</u>, is centrally initiated (Ter Braak, 1936), but little is known of the actual mechanism involved. A possible mechanism has been suggested by Lorente de Nó (1938), who postulated a neuron network that converted the continuous sensory input into a discontinuous nystagmic output. The salient feature of this mechanism was a trigger activated by some measure of the motor output. The possibility that the sensory input is involved directly in the initiation of the fast phase cannot be excluded, however, for Gutman et al (1963) have shown that the onset of the fast phase is hastened by electrical stimulation of the optic tract. Thus, although the compound eyes of *Carcinus* and the eyes of mammals have different optical mechanisms, their optokinetic responses are in many ways comparable.

BIBLIOGRAPHY

Alverdes, F. (1926). Stato-, Photo- and Tangoreaktionen bei zwei Garneelarten. *Z. vergl. Physiol. 4*, 699-765.

Alverdes, F. (1930). Tierpsychologische Analyse der intracentralen Vergänge, welche bei decapoden Krebsen die locomotorischen Reaktionen auf Helligkeit und Dunkelheit bestimmen. *Z. wiss. Zool. 137,* 403-75.

Barlow, H.B. (1963). Slippage of contact lenses and other artifacts in relation to the fading and regeneration of supposedly stable retinal images. *Q. Jl exp. Psychol. 15,* 36-51.

Bartley, S.H. (1951). The psychophysiology of vision. In *Handbook of experimental Psychology.* pp. 921-84. (Ed. Stephens, S.S.) New York: Wiley.

Bennett-Clark, H.C. & Evans, C.R. (1963). Fragmentation of patterned targets when viewed as prolonged after-images. *Nature, Lond. 199*, 1215-6.

Bergmann, F., Chaimovitz, M., Gutman, J. & Zelig, S. (1963). Optokinetic nystagmus and its interaction with central nystagmus. *J. Physiol., Lond. 168,* 318-31.

Bethe, A. (1895). Studien über das Centralnervensystem von *Carcinus maenas,* nebst Angaben über ein Verfahren der Methylenblaufixation. *Arch. mikrosk. Anat. EntwMech.* *44,* 579-622.

Bethe, A. (1897a). Das Nervensystem von *Carcinus maenas.* Ein anatomisch-physiologischer Versuch. 1. Theil. -1. Mittheilung. *Arch. mikrosk. Anat. EntwMech. 50,* 460-546.

Bethe, A. (1897b). Das Nervensystem von *Carcinus maenas.* Ein anatomisch-physiologischer Versuch. 1. Theil. -11. Mittheilung. *Arch. mikrosk. Anat. EntwMech. 50,* 589-639.

Boyce, P.R. (1967). Monocular fixation in human eye movement. *Proc. R. Soc. B. 167,* 293-315.

Brindley, G.S. & Merton, P.A. (1960). The absence of position sense in the human eye. *J. Physiol., Lond. 151,* 127-30.

Buddenbrock, W. von & Friedrich, H. (1933). Neue Beobachtungen über die kompensatorischen Augenbewegungen und den Farbensinn der Taschenkrabben *(Carcinus maenas). Z. vergl. Physiol. 19,* 747-61.

Burrows, M. (1967a). Ph.D. Thesis. St. Andrews University.

Burrows, M. (1967b). Reflex withdrawal of the eyecup in the crab *Carcinus. Nature, Lond. 215,* 56-7.

Burrows, M. & Horridge, G.A. (1967). In preparation.

Burtt, E.T. & Catton, W.T. (1961a), Diffraction images in the compound eye. *J. Physiol., Lond. 159,* 52P.

Burtt, E.T. & Catton, W.T. (1961b). Visual acuity in insects. *J. Physiol., Lond. 159,* 64-6 P.

Burtt, E.T. & Catton, W.T. (1962a). A diffraction theory of insect vision. 1. An experimental investigation of visual acuity and image formation in the compound eye of three species of insects. *Proc. R. Soc. B. 157,* 53-82.

Burtt, E.T. & Catton, W.T. (1962b). The resolving power of the compound eye. *Symp. Soc. exp. Biol. 16,* 72-85.

Bush, B.M.H. (1962). Proprioceptive reflexes in the legs of *Carcinus maenas* (L.). *J. exp. Biol. 39,* 89-106.

Bush, B.M.H. (1965a). Proprioception by the coxo-basal chordotonal organ, CB, in legs of the crab *Carcinus maenas. J. exp. Biol. 42,* 285-97.

Bush, B.M.H. (1965b). Proprioception by chordotonal organs in the mero-carpopodite and carpo-propodite joints of *Carcinus maenas* legs. *Comp. Biochem. Physiol. 14,* 185-99.

Bush, B.M.H. (1965c). Leg reflexes from chordotonal organs in the crab, *Carcinus maenas. Comp. Biochem. Physiol. 15,* 567-87.

Bush, B.M.H., Wiersma, C.A.G. & Waterman, T.H. (1964). Efferent mechanoreceptive responses in the optic nerve of the crab *Podophthalmus.* *J. cell. comp. Physiol.* *64,* 327-46.

Clark, G.P. (1896). On the relation of the otocysts to equilibrium phenomena in *Gelasimus pugilator* and *Platyonychus ocellatus.* *J. Physiol., Lond.* *19,* 327-43.

Clark, L.B. (1935). The visual acuity of the fiddler crab, *Uca pugnax.* *J. gen. Physiol.* *19,* 311-9.

Cochran, D.M. (1935). The skeletal musculature of the blue crab, *Callinectes sapidus,* (Rathbun). *Smithson. misc. Collns* *92,* (9), 1-76.

Cohen, M.J. (1960). A propriceptive system in the legs of the crab *Cancer magister.* *Anat. Rec.* *137,* 346.

Cooper, S., Daniel, P.M. & Whitteridge, D. (1955). Muscle spindles and other sensory endings in the extrinsic eye muscles; the physiology and anatomy of these receptors and of their connection with the brain stem. *Brain* *78,* 564-83.

Craik, K.J.W. (1940). Origin of visual after-images. *Nature, Lond.* *145,* 512.

Demoll, R. (1909). Über die Augen und die Augenstielreflexe von *Squilla mantis.* *Zool. Jb.* *27,* 171-212.

Dijkgraaf, S. (1955). Rotationssinn nach dem Bogengangsprinzip bei Crustaceen. *Experientia 11,* 407-9.

Dijkgraaf, S. (1956a). Über die kompensatorischen Augenstielbewegungen bei Brachyuren. *Pubbl. Staz. zool. Napoli 28,* 341-50.

Dijkgraaf, S. (1956b). Kompensatorische Augenstieldrehungen und ihre Auslösung bei der Languste *(Palinurus vulgaris). Z. vergl. Physiol. 38,* 491-520.

Ditchburn, R.W. & Fender, D.H. (1955). The stabilised retinal image. *Optica Acta 2,* 128-33.

Ditchburn, R.W. & Ginsborg, B.L. (1953). Involuntary eye movements during fixation. *J. Physiol., Lond. 119,* 1-17.

Drzewina, A. (1908). De l'hydrotropisme chez les crabes. *C. r. Séance. Soc. Biol. 64,* 1009-11.

Evans, C.R. & Piggins, D.J. (1963). A comparison of the behaviour of geometrical shapes when viewed under conditions of steady fixation, and with apparatus for producing a stabilised retinal image. *Br. J. physiol. Optics 20,* 1-13.

Fender, D.H. (1956). Ph.D. Thesis. Reading University.

Fender, D.H. (1964). The eye-movement control system: evolution of a model. In *Neural Theory and Modelling.* pp. 306-24. (Ed. Reiss, R.F.) Stanford Univ. Press.

Fender, D.H. & Nye, P.W. (1961). An investigation of the mechanisms of eye movement control. *Kybernetik 1,* 81-8.

Fender, D.H. & Nye, P.W. (1962). The effects of retinal image motion in a simple pattern recognition task. *Kybernetik 1,* 192-9.

Fermi, G. & Reichardt, W. (1963). Optomotor reactions of the housefly, *Musca domestica. Kybernetik 2,* 15-28. (English translation).

Fraenkel, G. & Gunn, D.L. (1940). *The orientation of Animals.* Oxford: Clarendon Press.

Fukuda, T. & Tokita, T. (1957). Über die Beziehung der Richtung der optischen Reize zu den Reflextypen der Augen- und Skelettmuskeln. *Acta oto-lar. 48,* 415-24.

Gavel, L.von (1939). Die "Kritische Streifenbreite" als Mass der Sehschärfe bei *Drosophila melanogaster. Z. vergl. Physiol. 27,* 80-135.

Götz, K.G. (1964). Optomotorische Untersuchungen des visuellen Systems einiger Augenmutanten der Fruchtfliege *Drosophila. Kybernetik 2,* 77-92.

Götz, K.G. (1965). Die optischen Übertragungseigenschaften der Komplexaugen von Drosophila. Kybernetik 2, 215-21.

Gutman, J., Bergmann, F., Chaimovitz, M. & Costin, A. (1963). Nystagmus evoked by stimulation of the optic pathways in the rabbit. Expl Neurol. 8, 132-42.

Hámori, J. & Horridge, G.A. (1966a). The lobster optic lamina. 1. General organisation. J. Cell Sci. 1, 249-56.

Hámori, J. & Horridge, G.A. (1966b). The lobster optic lamina. 11. Types of synapse. J. Cell Sci. 1, 257-70.

Hámori, J. & Horridge, G.A. (1966c). The lobster optic lamina. 111. Degeneration of retinula cell endings. J. Cell Sci. 1, 271-4.

Hámori, J. & Horridge, G.A. (1966d). The lobster optic lamina. 1V. Glial cells. J. Cell Sci. 1, 275-80.

Hanström, B. (1924). Untersuchungen über das Gehirn, insbesondere die Sehganglien der Crustaceen. Ark. Zool. 16, (10), 1-119.

Hanström, B. (1926). Eine genetische Studie über die Augen und Sehzentren von Turbellarien, Anneliden und Arthropoden. K. svenska Vetensk. Akad. Handl. (3). 4, (1), 1-176.

Harris, A.J. (1965a). Eye movements of the dogfish, *Squalus acanthus* (L.). *J. Physiol., Lond.* *177,* 21-2 P.

Harris, A.J. (1965b). Eye movements of the dogfish, *Squalus acanthus* (L.). *J. exp. Biol.* *43,* 107-30.

Hassenstein, B. (1951). Ommatidienraster und afferente Bewegungsintegration. (Versuche an dem Rüsselkäfer *Chlorophanus viridis.)* Z.verg *Physiol.* *31,* 301-26.

Hassenstein, B. (1954). Über die Sehschärfe von Superpositionsaugen (Versuche an *Lysmata seticaudata* und *Leander serratus).* *Pubbl. Staz. zool. Napoli* *25,* 1-8.

Hassenstein, B. (1958a). Die Stärke von optokinetischen Reaktionen auf verschiedene Mustergeschwindigkeiten. *Z. Naturf.* *13,* 1-6.

Hassenstein, B. (1958b). Über die Wahrnehmung der Bewegung von Figuren und unregelmässigen Helligkeitsmustern. *Z. vergl. Physiol.* *40,* 556-92.

Hassenstein, B. (1959). Optokinetische Wirksamkeit bewegter periodischer Muster (Nach Messungen am Rüsselkäfer *Chlorophanus* virid
Z. Naturf. *14b,* 659-89.

Hassenstein, B. & Reichardt, W. (1956). Systemtheoretische Analyse der Zeit-, Reihenfolgen- und Vorzeichenauswertung bei der Bewegungsperzeption des Rüsselkäfers *Chlorophanus.* *Z. Naturf. 11b,* 513-24.

Hecht, S. & Wald, G. (1934). The visual acuity and intensity discrimination of *Drosophila.* *J. gen. Physiol. 17,* 517-47.

Hecht, S. & Wolf, E. (1929a). The visual acuity of the honey bee and its relation to illumination. *Proc. natn. Acad. Sci. U.S.A.* 15, 178-85.

Hecht, S. & Wolf, E. (1929b). The visual acuity of the honey bee. *J. gen. Physiol. 12,* 727-60.

Helmholtz, H.von (1962). *Physiological Optics.* (Translated by Southall, J.P.C.) New York: Dover.

Holst, E.von & Mittelstaedt, H. (1950). Das Reafferenzprinzip (Wechselwirkungen zwischen Zentralnervensystem und Peripherie). *Naturwissenschaften 37,* 464-76.

Horridge, G.A. (1965). A direct response of the crab *Carcinus* to the movement of the sun. *Nature, Lond. 207,* 1413-4.

Horridge, G.A. (1966a). Optokinetic memory in the crab *Carcinus.* *J. exp. Biol. 44,* 233-45.

Horridge, G.A. (1966b). Perception of edges versus areas by the crab Carcinus. J. exp. Biol. 44, 247-54.

Horridge, G.A. (1966c). Optokinetic memory in the locust. J. exp. Biol. 44, 255-61.

Horridge, G.A. (1966d). Optokinetic responses of the crab Carcinus to a single moving light. J. exp. Biol. 44, 263-74.

Horridge, G.A. (1966e). Direct response of the crab Carcinus to the movement of the sun. J. exp. Biol. 44, 275-83.

Horridge, G.A. (1966f). Adaptation and other phenomena in the optokinetic response of the crab Carcinus. J. exp. Biol. 44, 285-95.

Horridge, G.A. (1966g). The optomotor response of the crab, Carcinus. In Information Processing in sight sensory Systems. (Ed. Nye, P.W.) pp. 57-74. Pasadena: California Inst. of Technology.

Horridge, G.A. (1967a). Study of a system, as illustrated by the optokinetic response. Symp. Soc. exp. Biol. 20. 179-98.

Horridge, G.A. (1967b). Perception of polarisation plane, colour and movement in two dimensions by the crab, Carcinus. Z. vergl. Physiol. 55, 207-24.

Horridge, G.A. & Sandeman, D.C. (1964). Nervous control of optokinetic responses in the crab Carcinus. Proc. R. Soc. B. 161, 216-46.

Horridge, G.A. and Shepheard, P.R.B. (1966). Perception of movement by the crab. *Nature, Lond. 209,* 267-9.

Keesey, U.T. (1960). Effects of involuntary eye movements on visual acuity. *J. opt. Soc. Am. 50,* 769-74.

Kreidl, A. (1893). Weitere Beiträge zur Physiologie des Ohrlabyrinthes (11. Mittheilung) Versuche an Krebsen. *Sber. Akad. Wiss. Wien (111.) 102,* 149-74.

Kuiper, J.W. (1962). The optics of the compound eye. *Symp. Soc. exp. Biol. 16,* 58-71.

Kunze, P. (1963). Der Einfluss der Grösse bewegter Felder auf den optokinetischen Augenstielnystagmus der Winkerkrabbe. *Ergebn. Biol. 26,* 55-62.

Kunze, P. (1964). Eye-stalk reactions of the ghost crab *Ocypode.* In *Neural Theory and Modelling.* pp. 293-305. (Ed. Reiss, R.F.) Stanford Univ. Press.

Lorente de Nó, R. (1938). Analysis of the activity of the chains of internuncial neurons. *J. Neurophysiol. 1,* 207-44.

McCann, G.D. & MacGinitie, G.F. (1965). Optomotor response studies of insect vision. *Proc. R. Soc. B. 161,* 369-401.

MacIntosh, W.C. (1860). Ph.D. Thesis. St. Andrews University.

McIntyre, A.K. (1939). The quick component of nystagmus. *J. Physiol., Lond.* *97,* 8-16.

Milne, L.J. & Milne, M. (1965). Stabilisation in the visual field. *Biol. Bull. mar. biol. Lab., Woods Hole* *128,* 285-96.

Palka, J. (1965). Diffraction and visual acuity of insects. *Science, N.Y.* *149,* 551-3.

Pardi, L. & Papi. F. (1961). Kinetic and tactic responses. In *The Physiology of Crustacea* Vol. 11. pp. 365-99. (Ed. Waterman, T.H.) New York: Academic Press.

Rademaker, G.C.J. & Ter Braak, J.W.G. (1948). On the central mechanism of some optic reactions. *Brain* *71,* 48-76.

Reichardt, W. (1957). Autokorrelations-auswertung als Funktionsprinzip des Zentralnervensystems. *Z. Naturf.* *12B,* 448-57.

Reichardt, W. (1961). Autocorrelation, a principle for the evaluation of sensory information by the central nervous system. In *Sensory Communication.* pp. 303-18. (Ed. Rosenblith, W.A.) New York: Wiley.

Reichardt, W. (1962). Nervous integration in the facet eye. *Biophys. J.* *2,* 121-43.

Reichardt, W, & Varjú, D. (1959). Übertragungseigenschaften im Auswertesystem für das Bewegungssehen (Folgerungen aus Experimenten an dem Rüsselkäfer *Chlorophanus viridis*). *Z. Naturf.* *14b*, 674-89.

Sandeman, D.C. (1964). Functional distinction between oculomotor and optic nerves in *Carcinus* (Crustacea). *Nature, Lond.* *201*, 302-3.

Sandeman, D.C. (1967). Excitation and inhibition of the reflex eye withdrawal of the crab *Carcinus*. *J. exp. Biol.* *46*, 475-85.

Schaller, F. (1953). Verhaltens- und Sinnesphysiologische Beobachtungen an *Squilla mantis*. *Z. Tierpsychol.* *10*, 1-12.

Schegtendal, A. (1934). Beitrag zum Farbensinn der Arthropoden. *Z. vergl. Physiol.* *20*, 545-81.

Schlieper, C. (1927). Farbensinn der Tiere und optomotorische Reaktionen. *Z. vergl. Physiol.* *6*, 453-72.

Schöne, H. (1952). Zur optischen Lageorientierung ("Lichtrückenorientierung") von Dekapoden. *Naturwissenschaften* *39*, 552-3.

Schöne, H. (1954). Statocystenfunktion und statische Lageorientierung bei dekapoden Krebsen. *Z. vergl. Physiol.* *36*, 241-60.

Schöne, H. (1959). Statocyst function and equilibrium orientation in crustaceans. *Anat. Rec.* *134*, 635.

Schöne, H. (1961). Complex behaviour. In The Physiology of Crustacea. Vol. 11. pp. 465-520. (Ed. Waterman, T.H.) New York: Academic Press.

Shepheard, P.R.B. (1966). Optokinetic memory and the perception of movement by the crab Carcinus. In The functional Organisation of the compound Eye. pp. 543-57. (Ed. Bernhard, C.G.) Oxford: Pergamon Press.

Sherrington, C.S. (1918). Observations on the sensual rôle of the proprioceptive nerve supply of the extrinsic eye muscles. Brain 41, 332-43.

Ter Braak, J.W.G. (1936). Untersuchungen ueber optokinetischen Nystagmus. Archs Néerl. Physiol. 21, 309-76.

Thorson, J. (1964). Dynamics of motion perception in the desert locust. Science, N.Y. 145, 69-71.

Thorson, J. (1966a). Small-signal analysis of a visual reflex in the locust. 1. Input parameters. Kybernetik 3, 41-53.

Thorson, J. (1966b). Small-signal analysis of a visual reflex in the locust. 11. Frequency dependence. Kybernetik 3, 53-66.

Tunstall, J. & Horridge, G.A. (1967). Electrophysiological investigation of the optics of the locust retina. Z. vergl. Physiol. 55, 167-82.

Van Tets, G.F. (1956). Thesis. University of British Columbia, Vancouver.

Varjú, D. (1959). Optomotorische Reaktionen auf die Bewegung periodischer Helligkeitsmuster. (Anwendung der Systemtheorie auf Experimente am Rüsselkäfer *Chlorophanus viridis.*) *Z. Naturf. 14b,* 724-35.

Vowles, D.M. (1966). The receptive fields of cells in the retina of the housefly *(Musca domestica)*. *Proc. R. Soc. B. 164,* 552-76.

Waterman, T.H. (1961). Light sensitivity and vision. In *The Physiology of Crustacea.* Vol. 11. pp. 1-64. (Ed. Waterman, T.H.) New York: Academic Press.

Waterman, T.H., Nunnemacher, R.F., Chace, F.A.Jr. & Clarke, G.L. (1939). Diurnal vertical migrations of deepwater plankton. *Biol. Bull. mar. biol. Lab., Woods Hole 76,* 256-79.

Waterman, T.H. & Wiersma, C.A.G. (1963). Electrical responses in decapod crustacean visual systems. *J. cell. comp. Physiol. 61,* 1-16.

Waterman, T.H., Wiersma, C.A.G. & Bush, B.M.H. (1964). Afferent visual responses in the optic nerve of the crab *Podophthalmus. J. cell. comp. Physiol. 63,* 135-55.

Westheimer, G. (1954). Mechanism of saccadic eye movements. *Archs Ophthal., N.Y. 52,* 710-24.

Wiersma, C.A.G. (1967). Integration in the visual pathway of Crustacea. Symp. Soc. exp. Biol. 20, 151-77.

Wiersma, C.A.G., Bush, B.M.H. & Waterman, T.H. (1964). Efferent visual responses of contralateral origin in the optic nerve of the crab Podophthalmus. J. cell. comp. Physiol. 64, 309-26.

Wiersma, C.A.G. & Yamaguchi, T. (1966). The neuronal components of the optic nerve of the crayfish as studied by single unit analysis. J. comp. Neurol. 128, 333-58.

Zuber, B.L. & Stark, L. (1966). Saccadic suppression: elevation of visual threshold associated with saccadic eye movements. Expl. Neurol. 16, 65-79.